A Multi-Predator Analysis: Comparing Trophic Niche Dimensions and Mercury Concentrations Among Four Sympatric Piscivores of Boreal Lakes

by

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ABSTRACT

Aquatic apex predators, like all predators, are an intrinsic part of a healthy ecosystem. They help stabilize food webs, as well as regulate and support strong biodiversity. In addition to being ecologically important, many predatory fish species are also of high socio-economic and cultural importance. Unfortunately, at the top of the trophic pyramid, apex predators are also at greater risk of accumulating harmful contaminants, such as mercury (Hg). With reports of rising Hg in boreal predatory fish species, the objective of this study was to compare and contrast the trophic ecologies and Hg concentrations of four sympatric piscivores of 27 boreal lakes across Ontario.

In Chapter 1, trophic relationships among sympatric burbot (*Lota lota*), lake trout (*Salvelinus namaycush*), northern pike (*Esox lucius*) and walleye (*Sander vitreus*) were investigated by using stable isotopes ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) to calculate metrics of trophic niche dimensions (position, size and shape) and trophic interaction. How each metric responded to varying environmental conditions was also explored. The trophic range utilized by all four species was similar, and the differences in trophic niche positions and dimensions observed were greatest when comparing species along a nearshore to offshore gradient. Overall, different environmental conditions had varying effects at different scales (i.e., population, paired-species, community); however, lake mean depth had the strongest and most consistent positive effect on niche dimensions and the dispersion of species within isotopic space. Deeper, clearer, less productive lakes (i.e., greater Secchi depth) supported greater niche segregation among these four species, while shoreline complexity had a negative effect on community trophic dispersion.

In Chapter 2, the relative importance of food web position ($\delta^{15}N$ and $\delta^{13}C$) and somatic growth rate (LGR) in explaining differences in muscle total Hg concentrations ([THg]) among the same four predatory fish species was explored. Ecosystem differences accounted for 44% of the total observed variability in [THg], and species differences accounted for 15%, of which approximately half could be attributed to differences in trophic positions and growth rates. Relative to $\delta^{13}C$ and LGR, $\delta^{15}N$ was the best predictor of [THg] among sympatric predators, but the best model included both $\delta^{15}N$ and LGR.

My thesis highlights how top predators in boreal lakes share trophic space and how their trophic interactions are modified by different lake habitat features. Identifying trophic variability among co-habiting top predators could help us better understand differences in [THg] among the important sympatric piscivores we rely on.

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CHAPTER ONE: TROPHIC NICHE SEGREGATION AND DIFFERENTIATION AMONG CO-HABITING APEX PREDATORS OF BOREAL LAKES

1.1 Introduction

The concept of an ecological niche was first introduced in the early 20th century by Joseph Grinnell (1917, 1924). He defined a species' niche as its functional role (behaviour) and occupied position (physical habitat) within the community. This definition was refined and sculpted by a number of successors (Pianka 1978), but most notably by George Hutchinson (1957a) who conceptualized the ecological niche as a "n-dimensional hypervolume"; a space not constrained to a specified number of environmental variables or dimensions. The full extent of this hypervolume that could theoretically be used by a species is called its fundamental niche and could only be fully occupied where the environment is phenotypically optimal, and detrimental interactions with other species (competition or predation) are non-existent. Of course, in nature, no organism is truly free of competition, predation, or changes in habitat structure, and quality, over time and space. All organisms occupy a smaller hypervolume, the realized niche, within the fundamental niche; a space which may shift in position, size and shape in response to various species interactions and changes in environmental conditions. Understanding the biotic and abiotic factors that shape the realized niche is of interest from the perspective of community structure and eco-evolutionary dynamics.

Interspecific competition is believed to be one of the primary forces shaping the realized niche. The competitive exclusion principle (Gause 1936) states that no two species niches can completely overlap; species can only coexist if they differ in their

ecology. This concept was demonstrated among populations of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Scandinavian lakes (Nilsson 1963, Langeland et al. 1991). Allopatric populations of both species were shown to utilize the same extent of food resources and habitat (pelagic and littoral) (Nilsson 1963) but, when found in sympatry, the two species exhibited interactive segregation, with Arctic char competitively excluded from the littoral zone during the summer months (Nilsson 1963, Langeland et al. 1991), forcing each species into distinct realized niches. During the winter months, however, brown trout were forced into a more pelagic environment, where they co-occurred with Arctic char. These studies were novel for their time and were among the first to demonstrate the impact of interspecific interactions on the niches of freshwater fishes. They also demonstrated how the realized niche can move, expand or contract with respect to environmental conditions (i.e., winter vs summer) without driving one species to extinction.

Earlier studies, such as the abovementioned, utilized stomach contents to determine fish diets, and determined habitat use based solely on conditions at the location where the fish was captured. The extent of the realized niche, however, could not be characterized further. Advances in the application of stable isotope ratios to ecological research have provided powerful tools which allow for time-integrated measures of diet (Peterson and Fry 1987, Vander Zanden and Rasmussen 1999, Newsome et al. 2007, Boecklen et al. 2011, Layman et al. 2012). An organism's body tissues (e.g., muscle, blood and hair) are synthesised from its diet, and thus reflect chemically what has been eaten over various time scales (Vander Zanden et al. 2015). Ratios of heavy to light stable isotopes of carbon ($^{13}C/^{12}C$; $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) can be used to infer energy flow and

trophic position in aquatic communities. In lakes, pelagic and benthic primary production have distinct $\delta^{13}C$ signatures (France 1995, Hecky and Hesslein 1995) and these signatures are largely retained as energy is transferred from producer to consumer, from prey to predator, up the food web. This allows us to trace fish back to their primary source of dietary carbon (pelagic and/or benthic). Unlike carbon, nitrogen tends to fractionate moving up the food web resulting in higher $\delta^{15}N$ with each successive trophic transfer (Minagawa and Wada 1984, Cabana and Rasmussen 1994). This step-wise enrichment allows for an individual's trophic position to be estimated. Together, the distribution of C and N isotopic ratios of individuals in C:N space can be used to infer the position, size, and shape of the realized trophic niche (Post 2002, Layman et al. 2007a, Newsome et al. 2007, Jackson et al. 2011).

To predict the potential ecological impacts of natural and anthropogenic disturbances on individual fish species and aquatic communities, we first need to understand how fish species coexist. Which abiotic and biotic factors facilitate niche separation, and to what extent can co-occurring species trophically interact successfully under different environmental conditions? This question is particularly important for co-habiting apex predators, which include some of the most economically and culturally valuable freshwater fish species in Canada (DFO 2012, Kuhnlein and Humphries 2017, Cott et al. 2018). These species have also frequently been introduced into lakes containing other resource-competing predators (Vander Zanden et al. 1999, 2003). In Ontario, Canada, there are over 250,000 lakes containing various combinations of predatory fish populations, which are experiencing a wide variety of environmental conditions. Most lakes in Ontario fall within the boreal shield ecozone and form an

excellent set of systems for studying the influence of abiotic and biotic factors on the realized trophic niches and co-existence of multiple fish species.

Four predatory fish species that are commonly found in boreal lakes are burbot (*Lota lota*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*) and walleye (*Sander vitreus*). These four species differ phylogenetically and ecologically with respect to thermal preferences, foraging strategies, and habitat use (Table 1.1, Fig. 1.1). Lake trout and burbot primarily occupy deeper offshore waters, northern pike primarily occupy shallower nearshore waters, and walleye are intermediate in habitat use. All four species utilize benthic habitats, but lake trout will also frequently use pelagic habitats (Fig. 1.1). Despite these differences in habitat preferences, all of these species are largely piscivorous as adults (Scott and Crossman 1973) and they form a trophic guild at the top of the food web. Most piscivorous fish are believed to be generalists in prey selection, and their diets originate from both benthic and pelagic primary production (Vander Zanden and Rasmussen 1996, Vadeboncoeur et al. 2002). As such we might expect these four species to interact through resource competition, despite their unique thermal, foraging and habitat preferences (Fig. and Table 1.1).

Comparative studies of the ecologies of fishes across boreal lakes need to take into consideration the potential for confounding environmental effects, because fish community compositions can differ greatly among lakes, and are related, in part, to the variation in environmental conditions. One way to control for this potentially confounding effect is to compare only co-habiting (sympatric) populations of the target species, but this may be challenging as the number of lakes with co-habiting populations of a particular suite of species will decline as the number of species of interest increases.

For Ontario lakes containing at least one apex predator species, it is estimated that < 5% contain three or more apex predator species, and such lakes tend to be large (> 1000 ha) (Johnson et al. 1977). Not surprisingly, studies comparing the trophic niches of multiple, co-habiting piscivore populations of boreal lakes are also quite rare, and to my knowledge, no study has examined and compared trophic niches of co-habiting lake trout, burbot, walleye and northern pike. Recent studies of trophic ecologies and habitat use of co-occurring lake trout, burbot, and northern pike in stratified subarctic lakes found evidence of overlap in their habitat use (Guzzo et al. 2016), but also found strong evidence for resource partitioning among them (Cott et al. 2011, Guzzo et al. 2016). Presumably, the inclusion of a fourth species, such as walleye, into the predator assemblage would increase the likelihood of species interactions, and may result in different patterns of resource partitioning.

The positions, sizes and shapes of realized trophic niches of aquatic consumers, as well as the trophic interactions among them, would be expected to depend, in part, on the environmental conditions they inhabit. In general, waterbodies with a wider diversity of habitats and resources should facilitate greater diversification, and thus allow larger realized niches for resident populations and/or greater divergence in niches among populations. Lake habitats are often described as a set of discrete zones, based on various dimensions: shallow vs deep, warm vs cold, pelagic vs benthic, nearshore (littoral) vs offshore (limnetic) (Fig. 1.1). In isotopic-based food web research, the pelagic-benthic axis has received the greatest attention. Though food chains are linear and may be categorized as pelagic or benthic, food webs composed of numerous food chains incorporate energy pathways from different zones, blurring the boundaries of discrete

energy flows (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). Fish contribute to the transfer of energy and nutrients by feeding across habitat boundaries, both horizontally (e.g., lake trout feeding in the littoral zone, Morbey et al. 2006), and vertically (e.g., burbot exhibit diel vertical feeding migration, Cott et al. 2015). The transfer of energy between habitats is referred to as ecological habitat coupling, and is influenced by the shape, size and quality of the environment. Smaller, shallower lakes with larger littoral areas are thought to allow a higher degree of habitat coupling (Wiens et al. 1985, Wetzel 1990, Polis et al. 1997, Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002), and therefore greater potential for trophic interaction among fish species. Alternatively, a more extensive littoral zone may actually de-couple energy flow if mobile coldwater species are unable to fully access the littoral zone (Dolson et al. 2009). Warmer environmental temperatures may also hinder habitat coupling, by hardening the thermal boundaries between different habitats (Tunney et al. 2014), and thereby shrinking trophic niche size and increasing trophic divergence among thermally distinct species. Foraging habits of visual predators can be influenced by water clarity, which can influence the overall trophic feeding range (Stasko et al. 2015) and degree of reliance on littoral vs pelagic energy sources (Tunney et al. 2018). To date, research on the relationships between trophic niche characteristics of aquatic consumers and the environmental conditions of the lakes they inhabit is still in the early stages. Much of it has been directed at the relationship between trophic niche position (i.e., food web position) and lake morphometry for one or two species. Broader questions of how other aspects of the trophic niche (e.g., size and shape) are related to multiple environmental factors in a multi-species assemblage have yet to be explored.

The objectives of my study were: i) to compare the trophic niche positions, sizes and shapes of lake trout, burbot, walleye and northern pike living in sympatry, and ii) to determine how these niche characteristics of each species, and niche interactions among them, are related to the environmental conditions of the waters they occupy. I met these objectives by sampling populations of all four species from each of 27 lakes across northern Ontario, characterizing the trophic niches of these populations using recently developed stable isotope niche metrics, and examining the relationships between niche metrics and environmental conditions of the lakes.

I hypothesised that i) trophic niche positions, sizes and shapes for co-habiting burbot, lake trout, northern pike and walleye based on stable isotope indices would reflect their purported habitat requirements and feeding ecologies based on earlier research; and ii) that species-specific niche metrics and trophic interactions between species would vary among ecosystems with respect to ecosystem size, morphometry, and productivity, and with respect to climatic conditions. Based on these hypotheses, I tested the following key predictions:

i) Trophic niche positions of these four piscivores will reflect a nearshore to offshore gradient as follows: northern pike (most nearshore), walleye, burbot, lake trout (most offshore).

ii) Because habitat complexity decreases from nearshore to offshore in boreal lakes, and because realized niche size is expected to increase with habitat complexity, then trophic niche size should decline from nearshore to offshore, being largest in northern pike and smallest in lake trout.

iii) Because all four species are known piscivores, the trophic elevation and the trophic range of their niches should be similar.

iv) Larger, deeper lakes with more complex shoreline structure offer a greater diversity of habitats and resources, resulting in greater resource partitioning and trophic niche separation among co-occurring species.

v) Lakes in warmer climates will have stronger thermal gradients from top to bottom, and this will accentuate habitat segregation among species due to species-specific thermal preferences, and result in greater resource partitioning and trophic niche separation.

vi) Because more productive lakes generally support a more abundant and diverse prey assemblage, all piscivores should be more selective in their diets in productive lakes, and have smaller trophic niches. Concurrently, more productive lakes also tend to have lower water clarity and are perceived as less complex by visual predators, reducing both population and community wide trophic diversity.

Table 1.1 Comparative ecologies of the adult stages of the four apex predator species examined (BUR = burbot, LT = lake trout, NP = northern pike, WALL = walleye). Thermal preference represents the optimal temperature range for adult fish survival and growth. Foraging tactics are defined as ambush (AM), pursuing (PR), grazing (GR) or stalking (ST).

Species	Habitat Use[b]	Thermal Preference[a] (°C)	Foraging Tactic[bd]	Primary Prey Detection Method	Diel Feeding Period
BUR	Benthic	15°C to 18°C[b]	PR/GR	Chemoreception / Vibration[f]	Nocturnal
LT	Benthopelagic	8°C to 12°C[c]	PR/GR	Visual	Diurnal
NP	Benthic-littoral	19°C to 23°C[c]	AM/ST	Visual	Diurnal[e]
WALL	Benthopelagic	18°C to 22°C[c]	PR	Visual[g]	Crepescular/ Nocturnal[h]

[a]Adult life stage, [b]Scott and Crossman 1973, [c]Christie and Regier 1988,[d]Coker et al. 2001, [e]Diana 1980, [f]Hinkens and Cochran 1988, [g]Ali et al. 1977, [h]Utne-Palm 2002

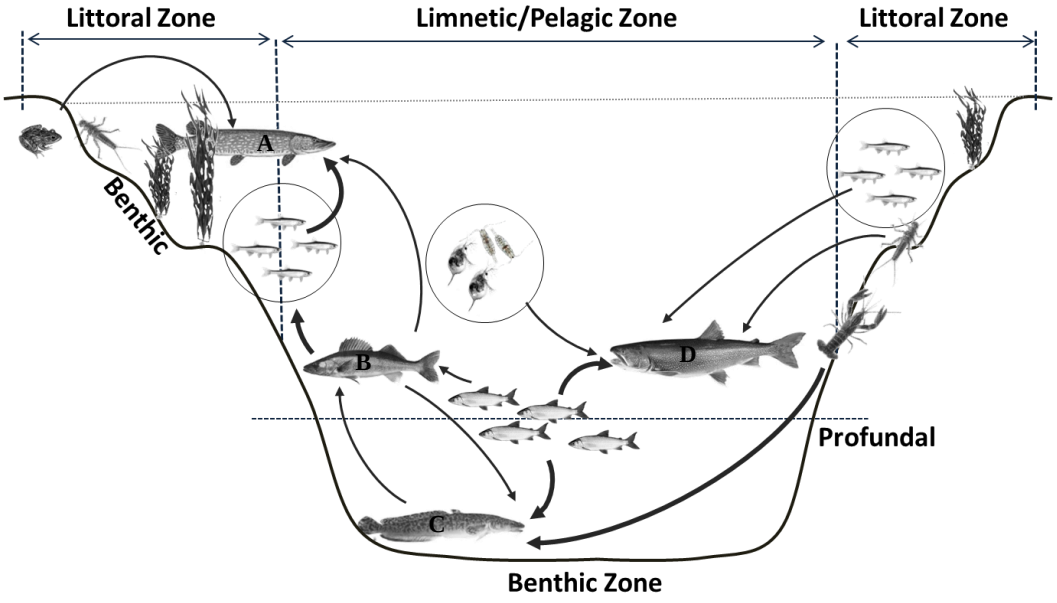

Figure 1.1 Cross-sectional schematic of a boreal lake. The littoral zone is the shallow nearshore area where the substrate is seasonally in contact with sunlight and warm water. The limnetic zone is the deeper, offshore area where sunlight does not penetrate to the bottom. Vertically, the lake is divided into the pelagic zone, defined as the upper water column, the profundal zone, defined as the lower water column (generally, below thermocline), and the benthic zone, defined as the water layer in contact with the substrate. Arrows indicate the direction of energy flow from prey to consumer, and arrow thickness is proportional to prey importance in each predators' diet based on earlier research. Consumers: A = northern pike, B = walleye, C = burbot, and D = lake trout.

1.2 Methods

Study lakes

Candidate lakes each containing populations of all four target species were identified and selected from across the Boreal Shield Ecozone in northwestern and northeastern Ontario. A total of twenty-seven lakes were successfully sampled ($n \geq 10$ fish / species / lake) and used for the current study (Fig. 1.2; Table 1.2). The lakes range in area from 2.6 to 348.1 km^2, and in mean depth from 3.2 to 38.3 m. They are dispersed along a latitudinal gradient from 46.2 °N to 52.2 °N, and fall within a climatic zone ranging from 1192 to 1680 growing degree days (GDD, >5°C). The study lakes are considered to have low to moderate nutrient levels and are largely classified as oligo-mesotrophic ([total phosphorus] 5 to 10 $\mu g/L^{-1}$, Table 1.2,Wetzel 2001). Two closely connected lakes treated as separate waterbodies in earlier surveys (Cassels and Rabbit Lakes, northeastern Ontario) were considered a single lake in the current study, and their data were pooled (Table 1.2).

Field sampling

Fish sampling was carried out between 2007 and 2017 (see Appendix Table A1) through joint efforts between the Laurentian University Cooperative Freshwater Ecology Unit (Sudbury, ON) and the Ontario Ministry of Natural Resources and Forestry's (MNRF) Broad-scale Monitoring Program (BsM). Most fish were sampled using overnight sets of multi-mesh, monofilament benthic gill nets of the NA1 configuration (Sandstrom et al. 2013). Supplementary sampling was carried out with baited long-lines (primarily for burbot) and angling gear (primarily for northern pike). Sampling targets

were a minimum of 10 fish per species per lake. Captured fish of each target species were selected to cover a wide range of body sizes, preferably encompassing 1 kg round weight which was used as a standard body size in subsequent analyses (see below). However, lake trout of ≤ 1 kg were rare or absent from the catch in some lakes (e.g., McInnes, McKay, Pagwachuan), and burbot ≥ 1 kg were also rare or absent from the catch in other lakes (e.g., Endikai, Goldie, Temagami) (Appendix Table A1). Each selected fish was lethally sampled following guidelines established by the Canadian Council on Animal Care, and under the approved animal use permits obtained through the MNRF (ARMS-ACC-97) and Laurentian University (2013-03-03).

All sampled fish were processed as follows. Total length (TL, mm), and round weight (RWT, g) were measured and recorded, and the sex and maturity were assessed by visual inspection of gonads. Stomach contents were qualitatively assessed for a subset of the individuals captured (n = 25 lakes). Prey items in the stomach were identified to the lowest taxonomic level possible and visually ranked as primary (largest proportion of stomach content volume) or secondary (all others) (Appendix Table A2). The primary and secondary prey proportions were then further categorised as fish, invertebrate or amphibian. Ageing structures (cleithra for northern pike, sagittal otoliths for all others) were removed, and a skinless, dorsal muscle sample (~ 30 g) was taken from the mid-body region above the lateral line. Cleithra were cleaned of all flesh by soaking in hot water, then allowed to air dry in paper envelopes, and sagittal otoliths were rubbed dry and stored in plastic vials. Fish muscle samples were placed in individually labeled whirl-pak bags and stored at -20°C prior to further processing.

Laboratory analysis

Each fish muscle sample was sub-divided into a smaller portion used for isotope analysis, and a larger portion used for mercury analysis (Chapter 2). The smaller portion was freeze-dried (Labconco Freezone 12) for seven days, ball-milled (Retsch MM400) to a fine powder and stored in glass scintillation vials. All ground samples were analyzed for carbon (C) and nitrogen (N) stable isotopes by continuous flow isotope ratio mass spectrometry (CFIRMS) at the Canadian Rivers Institute (CRI) Stable Isotopes in Nature Laboratory (University of New Brunswick, Fredericton, NB). The stable isotope ratios were expressed as the ratio of heavy to light isotopes relative to the same ratios in international reference standard materials (Pee Dee Belemnite for C, atmospheric nitrogen for N), as denoted by delta (δ):

$$(1) \qquad \delta^{H}X = \left[\left(\frac{R_{SAMPLE}}{R_{STANDARD}} - 1\right)\right] * 1000$$

where the superscript H is the atomic mass of the heavier isotope of element X (C or N), and R represents the ratio of the heavy isotope to light isotope ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) (Peterson and Fry 1987). All δ ratios were expressed in parts per thousand (‰). The mean ratio for C:N across all four fish species was below 4, suggesting low lipid content, thus lipid correction of the isotope data was not deemed necessary (Post et al. 2007).

Isotopic niche metrics

Characteristics of the trophic niches of each individual population (species x lake), as well as trophic interactions among the four species were inferred from isotopic niche metrics (Layman et al. 2007a, Jackson et al. 2011) (Table 1.3). At the population level, metrics were derived from the $\delta^{13}C$ and $\delta^{15}N$ data of individuals to infer:

(1) trophic niche positions (also called niche centroids, or food web positions) (mean $\delta^{13}C$ and mean $\delta^{15}N$ of population);

(2) the range of basal resources exploited by a population (CR, $\delta^{13}C$ range);

(3) the trophic range of a population (NR, $\delta^{15}N$ range);

(4) trophic niche size of a population (SEA_c, Jackson et al. 2011); and

(5) the evenness of distributed individuals in C:N space (SDNND).

All metrics were calculated using the R package SIBER (Jackson et al. 2011). Functions used to calculate SEAc were altered to expand the ellipse from the 1 SD default to 2 SD, in order to capture a larger proportion of the data. To quantify the extent to which species interact trophically, I calculated two interaction metrics (Table 1.3). The first was the total area (TA) of the piscivore assemblage convex hull, as mapped out in C:N space. This is an index of both the core niche space occupied by the piscivore assemblage, as well as the overall separation of the species in the assemblage. Studies have shown that convex hull (polygon) methods are sensitive to sample size, and this may bias the TA estimate (Syväranta et al. 2013). I reduced this effect by calculating TA from population trophic niche positions (mean $\delta^{13}C$, mean $\delta^{15}N$) rather than from individual $\delta^{13}C$ - $\delta^{15}N$ positions. This approach provides a conservative estimate of TA, but allows the sample size to be standardized at n = 4 across lakes. The second interaction metric was the distance between population centroids (DBC). This is the linear distance between trophic niche positions of two species in C:N space and is an index of the similarity of their food web positions, and the likelihood of trophic overlap or interaction.

Data acquisition: lake morphometry, productivity and climate

Lake morphometry and productivity data for all 27 lakes (Table 1.2) were acquired through the Ontario Ministry of Environment and Climate Change (MOECC) and the Ontario MNRF BsM program. The more southerly lakes tend to fall in regions of warmer climate relative to those located at higher latitudes, so I used growing degree days (GDD, cumulative degree days above 5°C), averaged over 15 years (2000 to 2015) as a measure of differences in climate and temperature across lakes. The average GDD values were obtained from Natural Resources Canada climate models (McKenney et al. 2011).

I calculated an index of shoreline convulsion (also called shoreline development), which has been used in previous studies to infer the extent of littoral zone (Dolson et al. 2009). I first calculated the shoreline development index (DI) (Hutchinson 1957b):

(2) $$DI = L/\sqrt{4\pi A}$$

where L is the shoreline length and A is the lake surface area. Shoreline lengths were determined digitally using ArcGIS at a fixed scale. A DI of 1 represents a perfect circle, and DI values greater than 1 indicate increasingly complex shorelines. Similar to Kent and Wong (1982), I found that the natural log of lake surface area was strongly correlated with the natural log of lake shoreline for my study lakes ($R^2 = 0.85$, $F_{(1,25)} = 147.6$, $p < 0.001$). As such, I computed the fractal ratio (FR) by incorporating a fractal dimension (D) in equation 2:

(3) $$FR = L^{1/D}/\sqrt{4\pi A}$$

where D is two times the slope of the relationship between ln(L) and ln(A) (when D > 1, DI is a biased measure of shoreline complexity, Kent and Wong 1982). The FR was not correlated with lake area and was used as an unbiased index of shoreline complexity in my analyses.

Data analysis

All data handling and statistical analyses were performed using the statistical computing package R 3.4.0 (R Core Team 2017). It was expected that some of the observed variability in isotopic ratios within and among piscivore populations would be due to ontogenetic effects (Werner and Gilliam 1984). I accounted for this variability in my analysis as follows. Linearized relationships between $\delta^{15}N$, and $\delta^{13}C$ vs Log_e (RWT) were examined at a population level (species by lake). Obvious outliers were further investigated, and all identified data points with both a studentized residual greater than 3 and a Cook's distance greater than the cut off (4/(n-k-1); n = sample size, k = number of independent variables) (Fox 1997), were either corrected for human error or removed. Less than 1% of data were removed. Both $\delta^{15}N$ and $\delta^{13}C$ values were standardized to a 1 kg mass using isotope ratio vs body size slopes in order to account for body size covariation (Romanuk et al. 2011) (Fig. 1.3).

To compare the four piscivores with respect to each of the trophic niche metrics (Table 1.3), I used linear mixed effects models (nlme, Pinheiro et al. 2017) with lake as a random block effect and species as a fixed effect. Where the overall species effect was statistically significant, I performed *post hoc* pairwise comparisons across all taxonomic pairs using Tukey's honestly significant difference (HSD) tests, to identify which particular species pairings were different. I employed the same methods to explore

separation in niche positions; DBC was analyzed with species pairing (six levels, e.g., lake trout – northern pike) as the fixed effect, and lake as the random effect. All niche metrics, except for trophic niche position (mean $\delta^{13}C$ and $\delta^{15}N$) and DBC, were $\log_e$ transformed for these analyses, to normalize the distribution of residuals.

Simple linear regressions and multiple regressions were used to examine the relationships between trophic niche metrics and environmental variation among lakes with respect to climate, ecosystem size and shape, and productivity. For each taxonomic group, trophic niche metrics (Table 1.3) were regressed against six $\log_e$ transformed lake-specific characteristics: surface area, mean depth, FR, GDD, latitude, and Secchi depth. The distribution of residuals was assessed for each simple linear model both visually and statistically using a Shapiro-Wilk normality test. Where assumptions of normality were violated, niche metrics were also $\log_e$ transformed. Next, I constructed similar models relating the niche interaction metrics, TA and DBC, to the same six lake-specific characteristics. Each model included either one or two lake characteristics as model parameters. Prior to fitting the models, I ran a Pearson correlation analysis among the six lake characteristics to identify any sources of collinearity and possible covariation. Any two variables which were found to be significantly correlated, with an absolute r value greater than 0.5, were not included in the same model. GDD was significantly correlated with mean depth ($r = 0.55$, $p < 0.01$), Secchi depth ($r = 0.53$, $p < 0.01$) and latitude ($r = -0.67$, $p < 0.001$), and FR was correlated with lake mean depth ($r = -0.50$, $p < 0.01$). As such, of the 21 possible one and two variable combinations, only 17 were used. I also included an additional intercept only model to act as a null model increasing my total model count to 18. Variables used in the multiple regression models were $\log_e$

transformed to linearize relationships and to meet the basic assumptions of normality and heteroscedasticity. I also centered and scaled all independent variables (Becker et al. 1988) to generate standardized regression coefficients, which could be directly compared to one another to determine which lake-habitat parameter in the model had the greatest effect on the metric being analyzed (Schielzeth 2010, Grueber et al. 2011).

I used an information theoretic approach to assess the relative importance of the six lake characteristics in predicting TA and DBC (Johnson and Omland 2004). All 18 models were ranked using a Second-Order Information Criterion (AIC_c), which is a variant of Akaike's Information Criterion (AIC). When sample size (n) is small, relative to the number of model parameters (k) (i.e. $n/K < 40$; Burnham and Anderson 2002) it is possible that AIC will over-fit by selecting a model with too many parameters. The AIC_c variant includes an additional bias-correction term that accounts for error due to small sample size. The smaller the AIC_c value, the greater the chance the model closely approaches reality, and the better the model. In addition to the AIC_c values, I also calculated delta AIC_c (Δ_i), Akaike weight (w_i), and adjusted R^2 (Adj- R^2) values for each model. The Δ_i is simply the AIC_c difference between each alternative model (AIC_{cj}) and the top ranked model (AIC_{ci}; $\Delta_i = AIC_{cj} - AIC_{ci}$); the best model has a $\Delta_i = 0$. The w_i is the estimated probability that model i is the best among the models compared. Akaike weight may also be used to calculate the evidence ratio (w_i/w_j), which provides a way of determining the relative likelihood of one model being better than another. A high evidence ratio will provide strong support for the best model, while a small evidence ratio may identify uncertainty in the selected model. Lastly, the Adj- R^2 represents the proportion of variance in the dependent variable that is explained by the model. The Adj-

R^2 is not thought to be useful in model selection (McQuarrie and Tsai 1998, Johnson and Omland 2004), but is a useful descriptive statistic, especially since the top ranked model may not actually be the strongest predictive model (Burnham and Anderson 2002). AIC_c models were built and ranked using R packages AICcmodavg (Mazerolle 2017) and MuMIN (Bartoń 2018). While all 18 models were fitted and ranked, I chose to display only single-parameter models, and two-parameter models which ranked above the intercept, and had a Δ_i of 4 or less (Table 1.6) (Burnham and Anderson 2002). A summary of all models ranked using AIC_c is presented in Appendix Table A3.

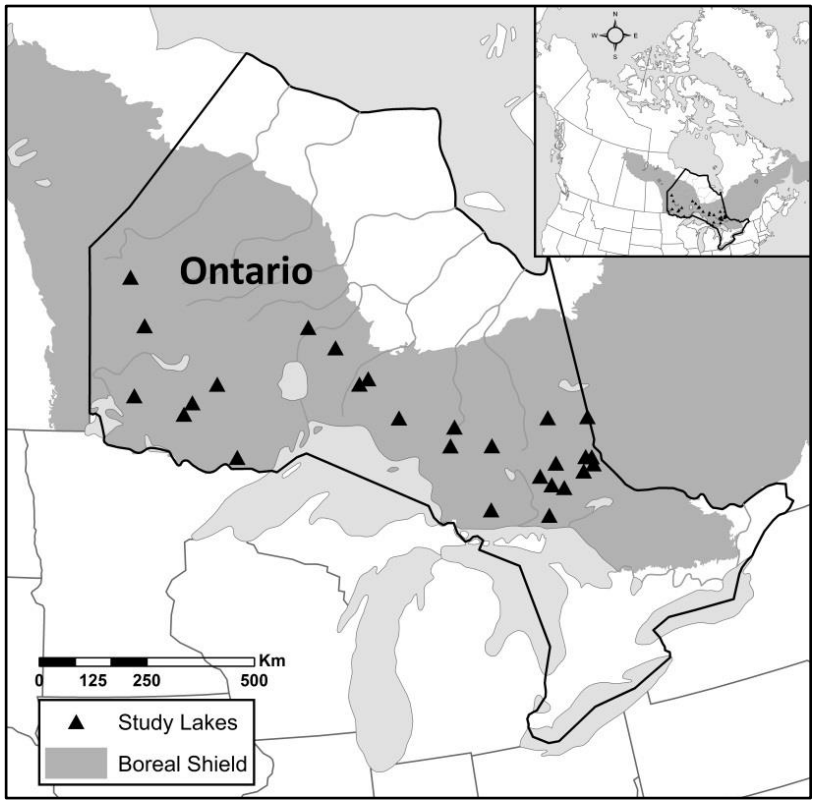

Figure 1.2 Location and distribution of study lakes across northern Ontario, Canada.

Table 1.2 Summary of study lake characteristics: coordinates (decimal degrees), mean annual growing degree days (GDD, > 5^0 C, 2000 - 2015), surface area (km^2), shoreline length (km), shoreline fractal ratio (FR), mean and maximum depth (m), and measures of productivity, total phosphorus (TP, µg/g) and Secchi depth (m).

Lake	Latitude	Longitude	Mean GDD	Area	Shoreline Length	FR	Mean Depth	Max Depth	TP	Secchi Depth
Anima Nipissing	47.25	-79.90	1524	20.5	173.4	1.40	13.7	76.2	3.1	9.4
Bending	49.32	-92.13	1513	11.5	94.6	1.30	12.5	45.8	5.9	4.6
Bigwood	46.84	-81.09	1554	2.7	33.4	1.44	6.5	58.0	5.3	6.8
Cassels-Rabbit	47.07	-79.72	1574	14.3	136.5	1.45	11.9	36.6	5.4	5.4
Endikai	46.59	-83.03	1662	5.9	24.5	0.80	29.0	48.2	3.8	5.8
Goldie	48.05	-83.90	1268	12.3	144.2	1.62	3.2	22.0	5.0	5.0
Kagianagami	50.93	-87.87	1192	75.9	424.8	1.25	8.9	45.0	7.9	6.2
Kwinkwaga	48.80	-85.34	1245	8.6	81.7	1.38	6.6	36.6	11.0	3.0
Mameigwess	49.54	-91.85	1491	53.1	134.6	0.75	16.1	50.0	5.7	7.6
McInnes	52.23	-93.76	1312	65.3	407.8	1.31	15.3	53.4	5.2	3.2
McKay	49.61	-86.44	1253	31.3	207.0	1.26	9.4	48.8	9.9	4.4
Missinaibi	48.42	-83.67	1334	77.1	273.9	0.95	19.2	94.0	6.9	4.2
O'Sullivan	50.43	-87.06	1197	42.9	168.5	0.95	8.4	45.7	10.5	3.7
Pagwachuan	49.70	-86.14	1267	27.0	79.4	0.76	18.0	54.9	6.9	5.5
Panache	46.24	-81.36	1679	80.1	302.9	0.99	15.4	56.4	4.4	6.9
Radisson	48.22	-80.76	1415	5.4	34.0	1.02	14.4	54.3	4.0	4.5
Raven	48.05	-79.55	1449	6.2	34.2	0.96	19.0	46.9	7.4	2.9
Rib	47.22	-79.72	1524	6.8	55.8	1.22	16.4	44.8	4.2	5.4
Rollo	47.89	-82.64	1393	8.1	40.4	0.93	14.5	53.0	7.2	3.8
Scotia	47.07	-80.83	1503	8.3	77.6	1.36	17.8	63.1	4.1	6.9
Stull	47.26	-80.83	1441	2.6	16.6	0.96	7.5	34.3	5.1	5.0
Sturgeon	49.90	-91.01	1442	214.1	1630.0	1.68	13.6	93.0	6.2	4.0
Temagami	46.97	-80.06	1601	209.7	1520.2	1.62	18.2	109.8	5.1	10.7
Titmarsh	51.25	-93.31	1393	9.7	34.9	0.77	13.6	49.4	6.0	3.8

Lake	Latitude	Longitude	Mean GDD	Area	Shoreline Length	FR	Mean Depth	Max Depth	TP	Secchi Depth
Trout	51.20	-93.32	1394	348.1	1220.7	1.10	14.0	47.3	5.4	5.8
Wanapitei	46.73	-80.74	1670	131.3	162.0	0.53	38.3	141.7	4.0	5.8
Winnange	49.74	-93.71	1528	26.3	165.59	1.20	24.2	115.2	4.5	8.5

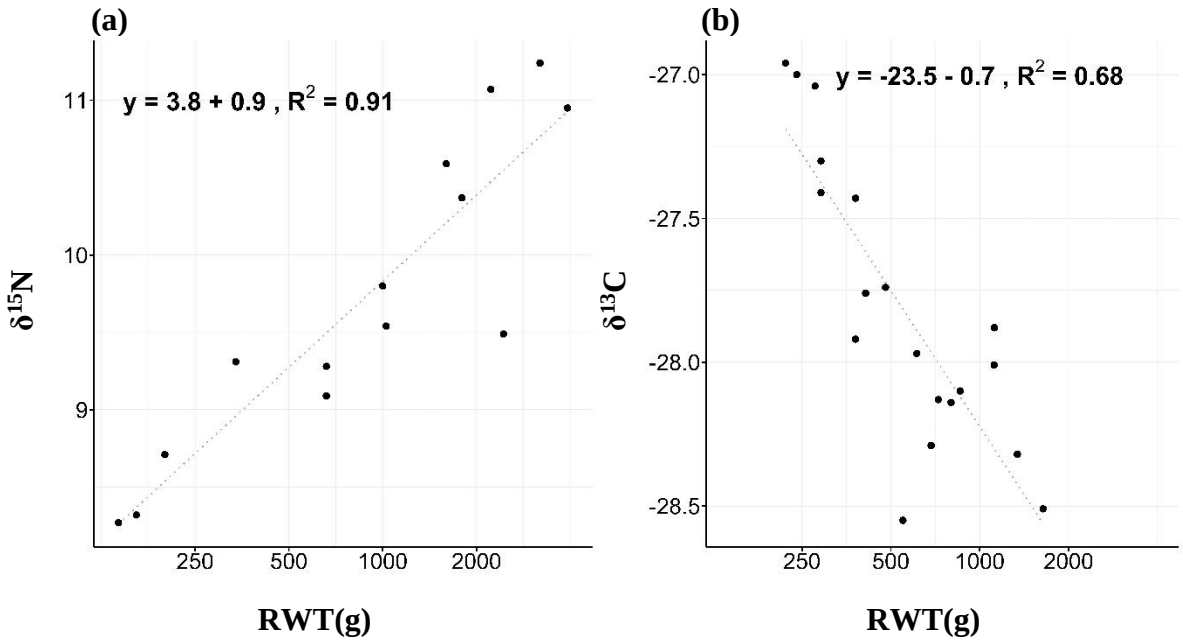

Figure 1.3 Examples of strong relationships between muscle isotope ratios and round weight (RWT, g) in study populations: (a) $\delta^{15}N$ in northern pike of Scotia Lake, (b) $\delta^{13}C$ in burbot of Stull Lake.

Table 1.3 Summary of quantitative measures of trophic ecology of populations and trophic interactions within the community based on stable isotope compositions.

Metric	Measure	Ecological Interpretation
Population-level		
Mean $\delta^{15}N$*	Mean $\delta^{15}N$ value for a population	Index of trophic elevation
Mean $\delta^{13}C$*	Mean $\delta^{13}C$ value for a population	Index of supporting primary production sources
CR	$\delta^{13}C$ Range	Estimate of exploited basal resources by a population, and an index of niche dimension (Layman et al. 2007)
NR	$\delta^{15}N$ Range	Estimate of a population's trophic length, and an index of niche dimension (Layman et al. 2007)
SEA_c	Standard Ellipse Area corrected for small sample size, estimated as the area of a bivariate ellipse capturing 2 SD of the individual $\delta^{13}C$ - $\delta^{15}N$ data, and corrected for small sample size	Index of a populations' trophic niche size (Jackson et al. 2011)
SDNND	Standard deviation of the Euclidean distances to each species' nearest neighbour in C:N space	Index of trophic evenness within a population (Layman et al. 2007)
Community-level		
TA	Convex hull area defined by the mean $\delta^{13}C$ and mean $\delta^{15}N$ coordinates of all piscivore populations	Conservative estimate of trophic niche space occupied by piscivore assemblage. Index of trophic diversity of species within the food web (Layman et al. 2007)
DBC	Euclidean distance between mean $\delta^{13}C$ and mean δ^{15} coordinates of two populations	Separation of trophic niche positions of two species, and an index of their potential trophic interaction (Turner et al. 2010)

** Together, mean $\delta^{15}N$ and $\delta^{13}C$ represent the mean overall trophic food web position of a population.*

1.3 Results

Qualitative stomach content analyses

Prey items from the stomach contents for fish captured from 25 lakes were classified as fish, invertebrate or amphibian. The primary identifiable prey item for all four piscivore species was most frequently fish, followed by invertebrates (Table 1.4). Amphibians were only identified from northern pike stomachs and were never classified as the primary prey. Walleye appeared to be the most specialized piscivore, with fish identified as the primary prey in 92% of stomachs, whereas burbot appeared to be the most generalized piscivore, with fish identified as primary prey in only 58% of stomachs (Table 1.4). Relatively few individuals contained a secondary identifiable prey item (12 burbot, 7 lake trout, 13 northern pike and 7 walleye), therefore only primary prey are presented in Table 1.4.

Summary of food web structure

The trophic niche metrics estimated for all four piscivore species at a standard 1 kg body size are summarised in Table 1.5. Burbot and lake trout had similar mean $\delta^{15}N$, and burbot and walleye had similar mean $\delta^{13}C$. Variability in trophic niche positions (mean $\delta^{15}N$ and mean $\delta^{13}C$) appeared to be greatest among burbot and lake trout populations. Trophic niche size (SEA_c), evenness (SDNND), and shape (CR, NR) were most variable across lakes for walleye. Despite the high variability in NR among walleye populations, walleye had the smallest mean NR of the four species, and lake trout the

largest. Northern pike populations were found to have the largest mean CR, SEA_c and SDNND, and burbot the smallest (Table 1.5).

Trophic niche positions among the four piscivores were significantly different in both the $\delta^{15}N$ ($F_{(3,78)} = 67.93$, $p < 0.0001$) and $\delta^{13}C$ ($F_{(3,78)} = 16.80$, $p < 0.0001$) dimensions. In the $\delta^{15}N$ dimension, lake trout and burbot were distinctly elevated relative to walleye and northern pike (Fig. 1.4). Comparisons of mean $\delta^{15}N$ for all species pairs were statistically significant ($p < 0.001$), except for comparisons of lake trout with burbot ($p = 0.99$) and walleye with northern pike ($p = 0.08$). Comparisons of mean $\delta^{13}C$ for all species pairs were statistically significant ($p < 0.05$), except for the burbot and walleye pairing ($p = 0.98$). Lake trout had the lowest $\delta^{13}C$ and northern pike the highest (Fig. 1.4). NR was not significantly different among species ($F_{(3,78)} = 0.93$, $p = 0.43$). The basal carbon range (CR), however, differed among species ($F_{(3,78)} = 7.82$, $p < 0.001$), but only for pairings with burbot. Burbot had a significantly lower CR than lake trout ($p < 0.05$), northern pike ($p < 0.001$), and walleye ($p < 0.01$) (Fig. 1.4). Niche size, inferred from SEA_c, also differed significantly among species ($F_{(3,78)} = 3.81$, $p < 0.05$), but only for the burbot and northern pike pairing ($p < 0.01$) (Fig. 1.4). The distribution of individuals within their niches, inferred from SDNND, did not differ among species ($F_{(3,78)} = 2.07$, $p = 0.11$).

The DBC was found to be significantly different among the six possible species pair combinations ($F_{(5,130)} = 8.23$, $p < 0.001$). The mean DBCs for burbot and northern pike (BUR.NP), and for lake trout and northern pike (LT.NP) were the largest (Fig. 1.5), and not significantly different from one another ($p = 0.75$), or from the DBC for lake trout and walleye (LT.WALL; $p > 0.05$). They were, however, significantly different

from the DBCs of the three remaining species pairs ($p < 0.05$). The smallest mean DBCs were for burbot and lake trout (BUR.LT), and for northern pike and walleye (NP.WALL) pairings (Fig. 1.5). The core niche space occupied by the four piscivore species combined (TA, Fig. 1.6) was variable among lakes, ranging in area from 0.25 to 8.5 ‰^{2} with a mean of 2.19 ‰^{2}.

Lake-habitat effects on food web ecology

Variation among lakes in the core realized niche space occupied by the four piscivores (TA) was best explained by models including Secchi depth and FR ($\Delta_i = 0.00$ and $w_i = 0.37$), and Secchi depth and lake mean depth ($\Delta_i = 0.39$ and $w_i = 0.30$) (Table 1.6). The small evidence ratio ($w_1/w_2 = 1.23$) suggests that these models have nearly equal strength. FR and lake mean depth were moderately correlated (Pearson, $r = -0.50$, $p < 0.01$), which may explain why both top ranked models were weighted similarly and explained similar amounts of variation (Adj-$R^2 = 0.37$ and 0.36, Table 1.6). Single parameter models with lake surface area and latitude ranked below the intercept-only model. TA increased with Secchi depth and lake mean depth, but declined with increasing FR (Table 1.6). The observed relationships between TA and lake characteristics may be driven equally by all piscivore species, by a single species, or the interaction between two or three species; thus, I also explored how lake-habitat variability influenced species-specific metrics of trophic ecology and trophic interactions.

Individual species niche metrics appeared to respond differently to the lake characteristics. The number of significant univariate relationships observed between trophic niche metrics and lake characteristics was highest for burbot, followed by lake trout, walleye, and lastly, northern pike. Of the six lake characteristics, mean depth,

Secchi depth and GDD best accounted for variation in the trophic niche metrics. Mean $\delta^{15}N$ was negatively related to Secchi depth for lake trout ($F_{(1,25)} = 5.40$, $p < 0.05$, Adj-$R^2 = 0.14$) and northern pike ($F_{(1,25)} = 4.46$, $p < 0.05$, Adj-$R^2 = 0.12$), and was negatively related to both latitude ($F_{(1,25)} = 11.92$, $p < 0.01$, Adj-$R^2 = 0.30$) and FR ($F_{(1,25)} = 5.38$, $p < 0.05$, Adj-$R^2 = 0.14$) for burbot. Mean $\delta^{13}C$ for burbot and walleye were positively related to mean depth ($F_{(1,25)} = 10.89$, $p < 0.01$, Adj-$R^2 = 0.28$; and $F_{(1,25)} = 12.42$, $p < 0.01$, Adj-$R^2 = 0.31$, respectively), Secchi depth ($F_{(1,25)} = 10.33$, $p < 0.01$, Adj-$R^2 = 0.26$; and $F_{(1,25)} = 7.96$, $p < 0.01$, Adj-$R^2 = 0.21$, respectively), and GDD ($F_{(1,25)} = 25.48$, $p < 0.001$, Adj-$R^2 = 0.48$, ; and $F_{(1,25)} = 14.80$, $p < 0.001$, Adj-$R^2 = 0.35$, respectively). Mean $\delta^{13}C$ for lake trout was also positively related to GDD ($F_{(1,25)} = 7.99$, $p < 0.01$, Adj-$R^2 = 0.2$). Only one significant relationship was observed for niche size (SEA_c); a positive relationship with Secchi depth for burbot ($F_{(1,25)} = 5.74$, $p < 0.05$, Adj-$R^2 = 0.15$). The NR for burbot populations increased with mean depth ($F_{(1,25)} = 5.18$, $p < 0.05$, adj-$R^2 = 0.14$), and also GDD ($F_{(1,25)} = 6.94$, $p < 0.05$, Adj-$R^2 = 0.19$). Lake trout CR narrowed with increasing GDD ($F_{(1,25)} = 9.63$, $p < 0.01$, Adj-$R^2 = 0.25$) and mean depth ($F_{(1,25)} = 4.40$, $p < 0.05$, Adj-$R^2 = 0.12$). In contrast, northern pike CR increased with mean depth ($F_{(1,25)} = 5.13$, $p < 0.05$, Adj-$R^2 = 0.14$). The evenness of the distribution of individual lake trout within a niche declined (SDNND increased) with increasing latitude ($F_{(1,25)} = 6.56$, $p < 0.05$, Adj-$R^2 = 0.18$).

The strength and ranking of relationships between separation of trophic niche positions (DBC) and the six lake characteristics varied greatly among the species pairings (Table 1.7). In general, all models predicting DBC of lake trout and any other species were weak ($w_i \leq 0.25$), and support for the top-ranked models was low ($\Delta_i \leq 4.5$) (Table

1.7). For the DBC of lake trout and burbot in particular, none of the models ranked higher than the null intercept model (Table 1.7). The DBC of lake trout and northern pike was positively related to latitude and lake mean depth, and the model including both of these predictors received the strongest support (Table 1.7). The DBC of lake trout and walleye was negatively related to shoreline complexity (FR) and positively related to Secchi depth, and the model with both of these predictors received the strongest support.

The DBC of burbot and northern pike increased with lake mean depth and Secchi depth, and narrowed with FR (Table 1.7). The best model included mean depth only, and four of the five top-ranked models also included mean depth as a predictor variable. The largest standardized coefficient was also observed for mean depth (Table 1.7). The DBC of burbot and walleye showed the strongest relationships with lake characteristics (Adj-$R^2 = 0.61$). Based on the standardized coefficients, all but Secchi depth appeared to have a significant effect on the DBC of burbot and walleye. However, of the six lake characteristics, the strongest predictors were mean depth and climate (Table 1.7). Overall, there was only empirical support for the top two models ($\Delta_i \leq 4$), which included mean depth and surface area, GDD and FR, respectively (Table 1.7). Both top models explained more than 50% of the observed variance (Adj-$R^2 \geq 0.6$).

The last comparison explored was between northern pike and walleye. The DBC between these two species was positively related to latitude, mean depth, Secchi depth, and surface area. The top two models had similar strengths ($w_i = 0.30$) and explained the same amount of variance (Adj-$R^2 = 0.30$). Both models included latitude, while the top ranked model also included mean depth, and the second model included Secchi depth.

Among the six lake characteristics, latitude was the predictor variable which most consistently had the largest coefficient.

Table 1.4 Percentages of sampled fish with identifiable prey items in their stomachs for which the primary prey (highest proportion of identifiable prey volume) was fish or invertebrates. Sample size (n) represents the total number of individual fish per species with identifiable stomach contents pooled across 25 study lakes.

Species	Sample size (n)	Fish as Primary Prey (%)	Invertebrates as Primary Prey (%)
Burbot	158	58	42
Lake trout	114	86	14
Northern pike	107	80	20
Walleye	121	92	8

Table 1.5 Ranges and means calculated for each population-level trophic metric (see Table 1.3) for burbot (BUR), lake trout (LT), northern pike (NP) and walleye (WALL) populations across n = 27 lakes.

Metric	Statistic	BUR	LT	NP	WALL
mean $\delta^{15}N$	Range	8.97 - 14.4	9.63 - 12.5	7.26 - 11.0	7.71 - 11.0
	Mean	10.9	10.9	9.13	9.52
mean $\delta^{13}C$	Range	-29.5 - -22.7	-34.0 - -24.7	-29.3 - -20.5	-29.7 - -24.3
	Mean	-26.3	-27.5	-25.5	-26.4
NR	Range	0.60 - 2.58	0.74 - 2.84	0.39 - 2.50	0.43 - 2.66
	Mean	1.37	1.49	1.29	1.27
CR	Range	0.64 - 4.15	0.99 - 3.85	0.73 - 5.11	0.64 - 5.54
	Mean	1.82	2.37	3.17	2.57
SEA_c	Range	0.83- 10.42	1.28 - 8.41	1.21 - 12.38	0.45 -13.51
	Mean	2.80	3.51	4.31	3.90
SDNND	Range	0.06 - 0.55	0.10 - 0.34	0.09 - 0.79	0.04 - 0.85
	Mean	0.18	0.21	0.26	0.24

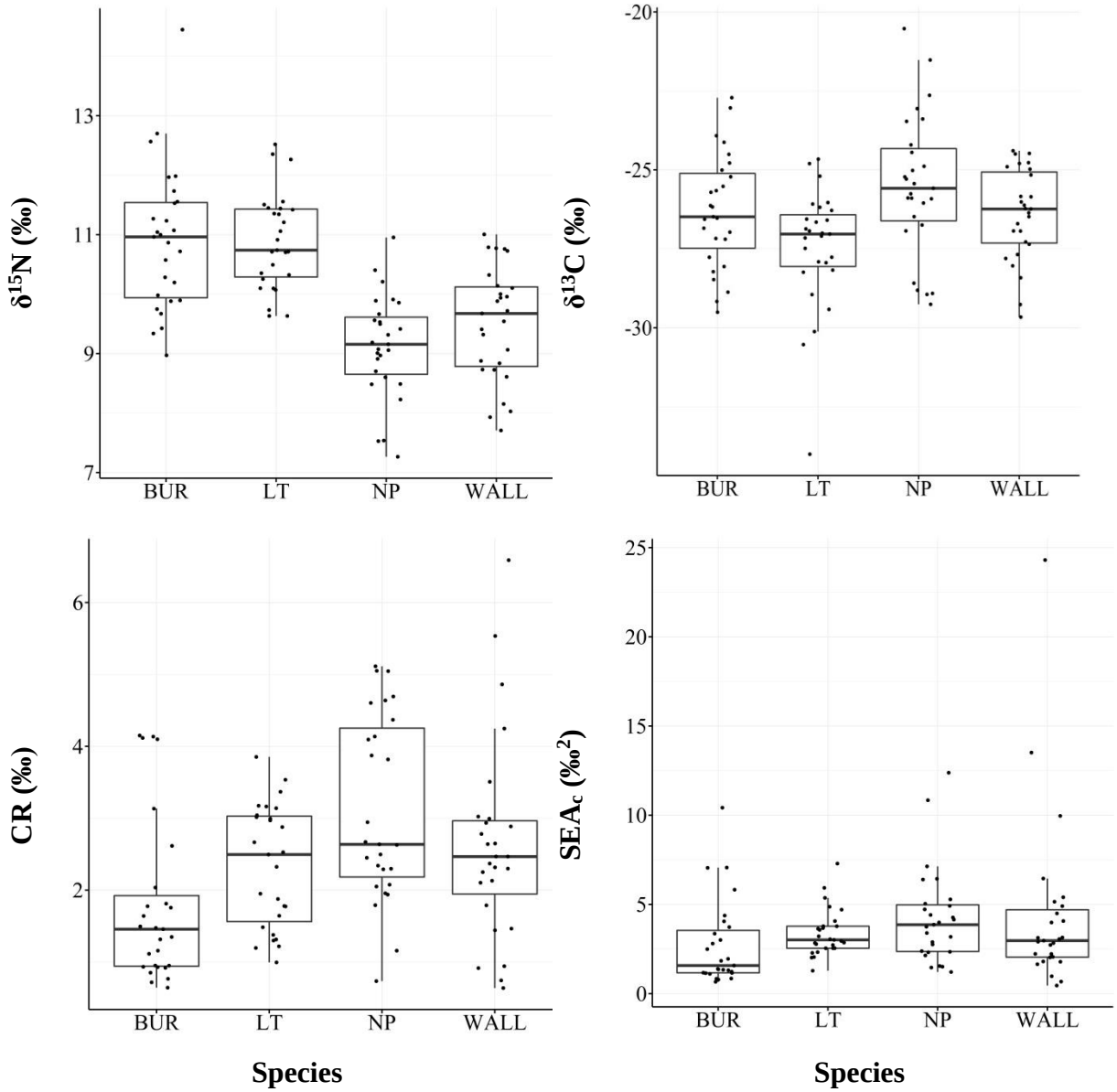

Figure 1.4 Box plots and data distribution of species-specific metrics ($\delta^{15}N$, $\delta^{13}C$, CR and SEA_c, defined in Table 1.3) found to be significantly different among co-habiting burbot (BUR), lake trout (LT), northern pike (NP) and walleye (WALL) populations. Points are jittered horizontally to improve visibility and represent individual populations (n = 27 lakes). The lower and upper hinges around the median correspond to the 25th and 75th percentiles, and the whiskers extend to the largest and smallest value within 1.5*IQR (inter-quantile range).

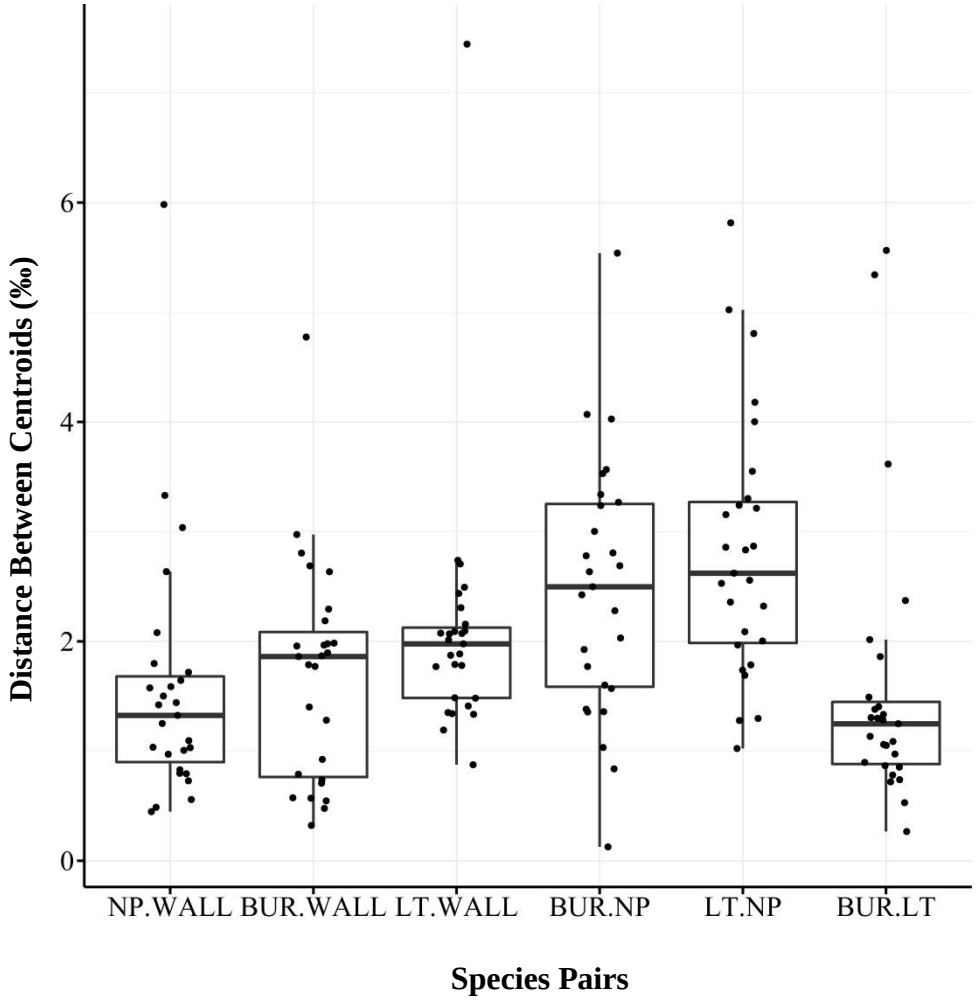

Figure 1.5 Box plots and data distribution of DBC (defined in Table 1.3) for species pairs of burbot (BUR), lake trout (LT), northern pike (NP) and walleye (WALL). Pairs are ordered by most nearshore to offshore combination. Points are jittered horizontally to improve visibility and represent individual populations (n = 27 lakes). The lower and upper hinges around the median correspond to the 25th and 75th percentiles, and the whiskers extend to the largest and smallest value within 1.5*IQR (inter-quantile range).

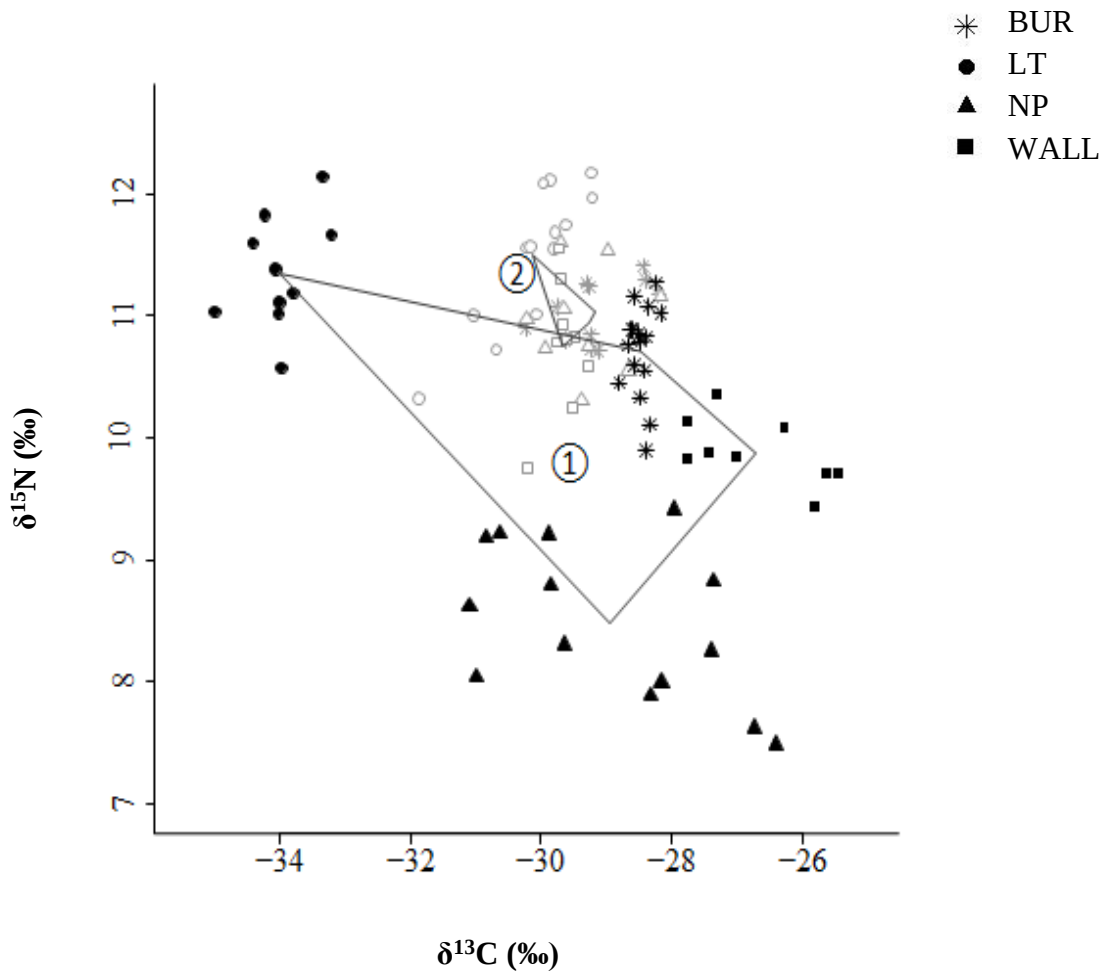

Figure 1.6 Community convex hulls (TA) for piscivore assemblages in two lakes are overlaid to show the broad variation in trophic diversity which exists: BUR = burbot, LT = lake trout, NP = northern pike, WALL = walleye. (1) Pagwachuan lake has the largest TA of all 27 study lakes, and (2) O'Sullivan Lake the smallest. Lighter, hollow, points represent individual fish from O'Sullivan Lake, and dark, opaque, ones from Pagwachuan.

Table 1.6 Summary of a subset of models ranked by second order Akaike Information Criterion (AIC_c) relating piscivore assemblage core niche area (TA) to lake mean depth (MeanD), surface area (SA), Secchi depth, shoreline fractal ratio (FR), growing degree days (GDD), and latitude. Only single parameter models and two parameter models ranked above the intercept model with a Δ_i value < 4 are presented. K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights, Adj-R^2 = adjusted R^2. Asterisks indicate a p-value < 0.05 for the null hypothesis that the coefficient is equal to zero (t-Test).

Parameters/Standardized Coefficients	Rank	K	AICc	Δ_i	w_i	Adj-R^2
Log(Secchi)(0.40*), Log(FR)(-0.38*)	1	4	58.35	0.00	0.37	0.37
Log(MeanD)(0.38*), Log(Secchi)(0.26)	2	4	58.74	0.39	0.30	0.36
Log(MeanD)(0.43*)	3	3	60.33	1.98	0.14	0.27
Log(MeanD)(0.47*), Log(SA)(-0.13)	4	4	62.09	3.74	0.06	0.27
Log(Secchi)(0.35*)	7	3	64.29	5.94	0.02	0.16
Log(GDD)(0.33*)	8	3	64.71	6.36	0.02	0.15
Log(FR)(-0.32*)	9	3	65.23	6.88	0.01	0.13
Intercept	10	2	67.46	9.11	0.00	0.00
Log(SA)(0.00)	15	3	70.00	11.65	0.00	-0.04
Log(Lat)(-0.09)	16	4	72.37	14.02	0.00	-0.07

Table 1.7 Summary of a subset of models ranked by second order Akaike Information Criterion (AIC_c) relating the Euclidean distance between population niche centroids (DBC) for each species pair to lake mean depth (MeanD), surface area (SA), Secchi depth, shoreline fractal ratio (FR), growing degree days (GDD), and latitude. Only single parameter models and two parameter models ranked above the intercept model with a Δ_i value < 4 are presented. K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights, Adj-R^2 = adjusted R^2. Asterisks indicate a p-value < 0.05 for the null hypothesis that the coefficient is equal to zero (t-Test).

Model Predictors and Coefficients	Rank	K	AICc	Δ_i	w_i	Adj R2
BURBOT - LAKE TROUT						
Intercept	1	2	57.09	0.00	0.22	0.00
Log(Lat)(-0.14)	2	3	58.43	1.33	0.11	0.01
Log(Secchi)(0.14)	3	3	58.43	1.34	0.11	0.01
Log(MeanD)(0.09)	4	3	59.11	2.01	0.08	-0.02
Log(FR)(-0.09)	5	3	59.14	2.04	0.08	-0.02
Log(GDD)(0.06)	6	3	59.38	2.28	0.07	-0.03
Log(SA)(-0.01)	7	3	59.64	2.54	0.06	-0.04
BURBOT - NORTHERN PIKE						
Log(MeanD)(0.60*)	1	3	83.11	0.00	0.34	0.23
Log(MeanD)(0.55*), Log(Secchi)(0.21)	2	4	84.74	1.63	0.15	0.23
Log(MeanD)(0.61*), Log(Lat)(0.08)	3	4	85.72	2.61	0.09	0.20
Log(FR)(-0.50*), Log(Secchi)(0.41)	4	4	85.85	2.75	0.09	0.20
Log(MeanD)(0.60*), Log(SA)(-0.02)	5	4	85.87	2.77	0.09	0.20
Log(FR)(-0.41), Log(GDD)(0.37)	6	4	86.64	3.53	0.06	0.18
Log(FR)(-0.44)	7	3	87.09	3.98	0.05	0.11
Log(GDD)(0.40)	8	3	87.93	4.82	0.03	0.08
Intercept	9	2	88.68	5.58	0.02	0.00
Log(Secchi)(0.33)	10	3	88.96	5.85	0.02	0.04
Log(SA)(0.15)	14	3	90.77	7.66	0.01	-0.02
Log(Lat)(0.00)	15	3	91.23	8.12	0.01	-0.04
BURBOT - WALLEYE						
Log(GDD)(0.42*), Log(FR)(-0.30*)	1	4	36.91	0.00	0.55	0.61
Log(MeanD)(0.48*), Log(SA)(-0.40*)	2	4	37.77	0.86	0.36	0.59
Log(GDD)(0.42*)	6	3	46.05	9.13	0.01	0.41
Log(MeanD)(0.37*)	9	3	51.82	14.90	0.00	0.27
Log(Lat)(-0.36*)	10	3	52.35	15.44	0.00	0.26
Log(FR)(-0.34*)	13	3	53.72	16.80	0.00	0.22
Log(SA)(-0.26*)	16	3	56.96	20.04	0.00	0.12
Intercept	17	2	58.90	21.98	0.00	0.00
Log(Secchi)(0.20)	18	3	58.93	22.01	0.00	0.05

Model Predictors and Coefficients	Rank	K	AICc	Δ_i	w_i	Adj R2
LAKE TROUT - NORTHERN PIKE						
Log(Lat)(0.17*), Log(MeanD)(0.14)	1	4	32.08	0.00	0.25	0.17
Log(Lat)(0.15)	2	3	32.92	0.84	0.16	0.09
Intercept	3	2	34.09	2.01	0.09	0.00
Log(MeanD)(0.12)	4	3	34.46	2.38	0.08	0.04
Log(SA)(0.11)	5	3	34.73	2.65	0.07	0.03
Log(FR)(-0.09)	8	3	35.54	3.46	0.04	0.00
Log(GDD)(-0.05)	9	3	36.26	4.18	0.03	-0.03
Log(Secchi)(0.02)	11	3	36.58	4.50	0.03	-0.04
LAKE TROUT - WALLEYE						
Log(FR)(-0.14*), Log(Secchi)(0.12)	1	4	28.22	0.00	0.16	0.14
Log(FR)(-0.12)	2	3	28.67	0.45	0.13	0.07
Intercept	3	2	29.07	0.85	0.11	0.00
Log(MeanD)(0.12)	4	3	29.07	0.86	0.11	0.05
Log(Secchi)(0.10)	5	3	29.62	1.41	0.08	0.03
Log(SA)(-0.06)	10	3	30.88	2.67	0.04	-0.01
Log(Lat)(-0.05)	12	3	31.15	2.93	0.04	-0.02
Log(GDD)(0.05)	13	3	31.17	2.95	0.04	-0.02
NORTHERN PIKE - WALLEYE						
Log(Lat)(0.38*), Log(Secchi)(0.26)	1	4	44.36	0.00	0.31	0.33
Log(Lat)(0.31*), Log(MeanD)(0.23*)	2	4	44.60	0.24	0.28	0.32
Log(SA)(0.21), Log(Lat)(0.20)	3	4	46.64	2.28	0.10	0.27
Log(SA)(0.28*)	4	3	47.54	3.18	0.06	0.19
Log(Lat)(0.28*)	5	3	47.75	3.39	0.06	0.19
Log(SA)(0.29*), Log(FR)(-0.15)	6	4	47.84	3.48	0.05	0.23
Log(MeanD)(0.20)	11	3	51.36	7.00	0.01	0.07
Intercept	12	2	51.83	7.47	0.01	0.00
Log(FR)(-0.14)	13	3	52.84	8.48	0.00	0.02
Log(Secchi)(0.11)	14	3	53.39	9.03	0.00	0.00
Log(GDD)(-0.02)	17	3	54.35	9.99	0.00	-0.04

1.4 Discussion

In this study I assessed the within- and among-species trophic diversity for four co-occurring predators from 27 lakes. Overall, trophic niche positions, sizes, and shapes differed only slightly among the four ecologically dissimilar piscivores, with the largest differences observed when comparing trophic niche dimensions between nearshore and offshore species. This study is unique in that it is the first, to my knowledge, to compare the trophic ecology of four sympatric predators across a wide breadth of environmental conditions (lake morphology, productivity, climate and latitude). How environmental conditions influenced trophic diversity among my study species was different for each scale of observation (i.e., individual, paired-species and community). Generally, lake mean depth was the most consistent and strongest predictor of trophic variability among species at all scales. At the individual species level, Secchi depth and GDD were also important influences on trophic diversity, and at the community level, shoreline structure also influenced trophic diversity and niche separation. Latitude and surface area had the weakest effects on trophic diversity among predators, but were important when comparing trophic niche positions of paired species.

Trophic niche position, size and shape

As predicted, the trophic niche positions among these four species followed an offshore to nearshore gradient, with lake trout having the most pelagic $\delta^{13}C$ signature and northern pike the most littoral. The mean $\delta^{15}N$ position among the four species, however, was surprisingly different. For a standardized body size, lake trout and burbot held identically high trophic positions compared to northern pike and walleye. The diverging trophic positions might be due to fish age. Northern pike and walleye are faster growing

species and are likely to be younger than lake trout and burbot at 1 kg (Chapter 2). Stepwise changes in $\delta^{15}N$ have been found to be more strongly related to age than diet in some walleye populations (Overman and Parrish 2001), suggesting that ^{15}N enrichment over time may have a non-dietary component. While $\delta^{15}N$ in lake trout and mussels was not positively related to age (Minagawa and Wada 1984, Kiriluk et al. 1995), fractionation during the transfer of nitrogen between amino acids (i.e., transamination or deamination) could result in faster ^{14}N excretion rates, and increased ^{15}N enrichment, over time (Macko et al. 1986). Therefore, metabolic processes influencing the rate of fractionation in different species may explain why four co-occurring piscivores with similar nitrogen ranges (NR) had variable mean $\delta^{15}N$ signatures.

Trophic niche size (SEA_c) among the study species followed a gradient from nearshore to offshore, but not in the manner in which I had predicted. Northern pike had the largest trophic niche, but lake trout did not have the smallest; rather, burbot had the smallest trophic niche. Outside of the spawning or seasonal migration window, burbot are believed to be a relatively sedentary species (McPhail and Paragamian 2000). Therefore, burbot would not be expected to exploit the same extent of basal resources compared to the other predators in my study, and consequently, the realized trophic niche boundaries for burbot are smaller. A smaller home range would also support the significantly smaller carbon range (CR) observed in burbot. Similar to burbot, northern pike are also often classified as a relatively sedentary species (Diana 1980), preferentially inhabiting and feeding in nearshore areas in lakes. However, radio-telemetry studies have shown that northern pike may actually travel long distances within a lake to utilize a diverse range of habitats (Chapman and Mackay 1984), and large northern pike utilize both open water

and vegetated nearshore areas (Grimm 1981). Based on the log-linear relationship between fish body length and weight, a 1 kg northern pike would be considered large according to Grimm's (1981) definition (> 54 cm fork length), and therefore northern pike in my study could exploit the largest carbon range due to the species' thermal tolerance for both cool offshore and warm nearshore water temperatures.

The observed separation of trophic niche positions (inferred from DBC) also followed expectations based on the nearshore to offshore gradient of these species. Walleye niche positions were close to those of northern pike, and burbot niche positions close to those of lake trout, supporting the expected inter-species interactions based on preferential feeding habitat (Scott and Crossman 1973). Overall, as an intermediate species, which commonly feeds in varied habitats (Scott and Crossman 1973), walleye were more likely to trophically interact with all three predators. The distances between paired species niches and the overall trophic volume (TA) of the piscivore assemblage, however, were quite variable across lakes indicating that the degree to which species interact trophically is dependent on their environment, supporting the intermittent use of alternate habitats by nearshore (e.g., northern pike feeding offshore, Chapman and Mackay 1984) and offshore (e.g., lake trout feeding nearshore, Morbey et al. 2006) species.

Effect of lake characteristics on trophic diversity

Principles of landscape ecology support the theory that larger heterogeneous habitats sustain greater species richness (MacArthur and Wilson 1967). Similarly, larger lakes would be expected to facilitate greater trophic diversity among predatory fish due to the greater diversity of available habitats and resources. Smaller, shallower lakes exhibit

stronger habitat coupling (Wiens et al. 1985, Wetzel 1990, Polis et al. 1997) due to higher levels of productivity, but also because of the increased access to larger more productive benthic habitat (Hanson and Leggett 1982, Schindler and Scheuerell 2002). Greater access to benthic or littoral habitat to mobile predators would promote species interaction by lessening niche separation among species. As such, I predicted that increasing lake size (mean depth and/or area) and shoreline complexity would result in an increase in community trophic diversity (TA) and greater niche separation among species (DBC).

I found that lake morphometry did have a strong effect on TA and DBC, as well as individual species trophic diversity, but predominantly with respect to depth and shoreline structure. Contrary to earlier studies (Vander Zanden et al. 1999, Bartels et al. 2016, Johnston et al. 2018), I did not find that lake surface area on its own had a strong effect on individual or community trophic diversity. When coupled with mean depth, surface area had a negative effect on niche separation between burbot and walleye. In an earlier study of north temperate lakes, maximum trophic positions of northern pike, walleye, lake trout, and largemouth bass (*Micropterus salmoides*) were found to be positively related to lake volume (Post et al. 2000), suggesting volume or basin shape might have also been good lake characteristics for predicting trophic segregation among predators. Independently, I found that deeper lakes had more expansive TA, possibly due to wider thermal boundaries influencing resource segregation among species (Brandt et al. 1980). The expansion of TA with increasing depth may have been driven by niche separation between burbot and northern pike, and between burbot and walleye, which both increased with depth.

The accessibility hypothesis (Dolson et al. 2009) holds that lakes with more reticulate shorelines have a larger extent of littoral habitat that is inaccessible to coldwater species (e.g., lake trout and burbot). If true, we would expect to see stronger niche separation between littoral and limnetic species in lakes with larger FR. I observed the opposite; contrary to my prediction, as FR increased, TA declined, therefore the trophic niche separation among all four species was reduced in more reticulate lakes. Lakes with more complex shorelines might support more diverse and abundant prey, allowing predators to feed on similar prey items, potentially explaining the smaller TA observed. At the individual species scale, burbot trophic elevation (inferred from $\delta^{15}N$) declined with increasing FR, suggesting that burbot may feed lower in the food chain in more structured lakes. Interestingly, FR had the strongest effect on niche dispersion (TA) and separation (DBC) when included in models with either climatic (GDD or latitude) or productivity / clarity (Secchi depth) predictor variables.

Lakes that are more productive typically support a more abundant and diverse prey assemblage (Dodson et al. 2000), allowing predators to specialize on preferred prey, resulting in a uniform diet among individuals, and smaller trophic niches. My index of productivity, Secchi depth, is also an index of visibility, and thus observed relationships between trophic niche characteristics and Secchi depth should be considered both from the perspective of prey abundance (linked to productivity), and predator-prey encounter rates (linked to visibility) (Turesson and Brönmark 2007). In terms of the visual environment, I expected that trophic ecologies of burbot and walleye would be less influenced by water clarity than trophic ecologies of lake trout and northern pike. This is because burbot is primarily a nocturnal feeder, relying on chemosensory and vibration

cues to locate prey (Hinkens and Cochran 1988). Similarly, walleye have specialized retinas adapted to scotopic and turbid environments (Ali et al. 1977) that allow them to feed successfully over a wide range of water clarities. My predictions regarding niche size and lake productivity only held for one species; burbot niche size (inferred from SEA_c) increased with Secchi depth, suggesting that their niches were smaller in the more productive lakes. Previous research on boreal lake food webs has found that relationships between trophic niche size and Secchi depth are quite variable among fish species, being evident in some piscivores but not others (Stasko et al. 2015), and not evident in benthivores (Johnston et al. 2018).

In contrast, I found that trophic niche position showed stronger relationships with Secchi depth than did niche size. Trophic elevation (inferred from mean $\delta^{15}N$) of both northern pike and lake trout declined with increasing Secchi depth, and reliance on benthic production (inferred from mean $\delta^{13}C$) of both burbot and walleye increased with increasing Secchi depth. The former result suggests that less productive lakes may have fewer food chain links leading to these piscivores, but a mechanism related to the visual environment is less evident. Interestingly, a similar decline in $\delta^{15}N$ with increasing Secchi depth has also been reported for the benthivore white sucker (*Catostomus commersoni*) in boreal lakes. The latter result suggests that burbot and walleye both feed more littorally in less productive lakes, a trend also seen in white sucker (Johnston et al. 2018) and Eurasian perch (*Perca fluviatilis*) (Bartels et al. 2016). In contrast, Tunney et al. (2018) found that walleye reliance on littoral production declined with increasing water clarity in boreal lakes, but examined lakes with fewer co-habiting piscivore species and covering a wider range of water clarities than my study. For the piscivore assemblage

as a whole, I found that interspecific trophic diversity (inferred from TA) expanded with declining productivity and/or increasing water clarity as predicted, however, the effects of productivity on TA were strongest when coupled with depth or shoreline structure, suggesting that the environmental influences on piscivore trophic interactions are multidimensional.

Because fish are ectotherms with variable physiological tolerances for different temperature ranges (Scott and Crossman 1973), it comes as no surprise that thermal gradients play a strong part in shaping the trophic ecology of a diverse assemblage of species like the one in my study. I had predicted that lakes in warmer climates would have stronger thermal gradients in the water column, which would result in greater trophic niche separation among my study species. Indeed, TA increased with GDD, supporting my prediction; however, its effect was generally weaker than effects attributed to Secchi depth and mean depth. This may be in part a result of the narrow climate gradient in which my study lakes fall. The expansion in TA due to GDD that I observed was primarily driven by greater niche separation between burbot and walleye with increasing GDD. Both of these species feed primarily on rocky shoals (Edsall et al. 1993), but in warmer waters, despite nocturnal vertical feeding migration, burbot will tend to remain in deeper, cooler waters (Cott et al. 2015), provided there is sufficient preferred habitat. Warmer climates create warmer epilimnia, thus reducing the suitability of nearshore zones as foraging habitat for coldwater species such as lake trout (Tunney et al. 2014), and resulting in narrower $\delta^{13}C$ ranges. The extended trophic range observed for burbot with warmer air temperatures was unexpected; burbot may be feeding on prey species from lower trophic levels instead of relying on fish as temperatures increase.

Most studies that focus on the effects of climate in general, and temperature in particular, on freshwater fish focus on one or two species, and it is still unclear how interspecific competition and resource partitioning among predators may be affected. How ectotherms will respond to long-term shifts in both the mean and variance in temperatures is predicted to be variable (Vasseur et al. 2014). For example, lake trout have been shown to feed further offshore and in deeper colder waters during periods of warmer summer temperatures (Tunney et al. 2014), resulting in habitat de-coupling (Dolson et al. 2009). Climate change has resulted in earlier ice-off on temperate lakes bringing about a longer spring period (Guzzo and Blanchfield 2016). An extended spring provides an extended opportunity for lake trout to feed on littoral prey and emerging invertebrates before retreating to deeper habitat as temperatures rise above 15°C. This would suggest that habitat coupling during the open-water season may not necessarily be lost under a warming climate (Tunney et al. 2014), but rather shift with phenology. Longer spring access to littoral areas by lake trout may result in increased seasonal interspecific competition with walleye and northern pike, which also utilize nearshore areas in the spring. These prolonged interactions and their effects on the community's trophic diversity, however, have not been previously investigated.

Changes to a community's environment can result in habitat decoupling, which could cause instability in the food web due to habitat fragmentation (Layman et al. 2007b), rendering more selective species (e.g., lake trout) more susceptible to extinction. It may also, however, promote ecological habitat coupling by increasing seasonal access to macro-habitats (Guzzo and Blanchfield 2016), increasing the likelihood of resource competition among predators. While predators are indeed resilient and somewhat

adaptable to habitat or thermal change (Brandt et al. 1980), they do run the risk of extinction if pushed beyond their physiological limits, especially cold-water species like burbot and lake trout. While changes to a predator's trophic niche may not lead to immediate extinction, other effects of a changing niche size or range could have deleterious implications. For example, in lakes where burbot and lake trout niches overlapped (e.g., Radisson and Winnange), large burbot were harder to capture, and smaller, older burbot were more abundant. The slower growth rate observed in such lakes could result from interspecific competition with lake trout (Tonn et al. 1986, Persson 1988). Slower growth renders a fish more susceptible to predation over a longer portion of its lifespan. Therefore, in a globally changing environment, it is important that trophic ecology studies consider not only the abiotic effects (e.g., lake morphometry and temperature), but also the biotic interactions that exist between species, which may play an important role in shaping their trophic niches.

Conclusion

In multi-predator boreal lakes, the realized trophic niche structure of the piscivore assemblage, as well as its component species, appears to generally agree with habitat and thermal requirements identified for these species in earlier research. Although dissimilarity among co-occurring species allows them to live in sympatry, it is evident from my study that changes to the environment, physical and chemical, can influence their potential for trophic interactions. Environmental gradients affect trophic niche diversity differently depending on the scale of observation; therefore, it is important to consider the broader community when trying to understand how our changing environment will affect the feeding ecology and life history of the species we rely on.

Future Studies

For future studies comparing assemblages of ecologically distinct species using isotopic metrics, I would suggest standardizing fish both to a common size and age to ensure trophic position estimates are not skewed by possible differences in fractionation over time. Studies carried out in northern climates should also consider seasonal patterns in trophic diversity. Most studies collect fish samples during the open-water season when logistics of field sampling are easiest, but overlap in habitat and resource use is probably greatest in winter when water temperatures are relatively uniform, and fish are not constrained by thermal stratification. Interspecific competition is likely to be greater in the winter and resource separation different (Langeland et al. 1991). It would also be interesting to compare the isotopic signatures of sympatric species using a tissue with faster turnover rates (e.g., blood or liver) between seasons to further capture how species co-exist trophically. Lastly, the inclusion of other physical parameters such as lake volume or relief/topography could also prove to be useful, given how strongly trophic niche size and shape are linked to lake morphometry and habitat structure.

CHAPTER 2: FACTORS AFFECTING INTERSPECIFIC VARIABILITY IN MERCURY BIOACCUMULATION AMONG FOUR CO-HABITING BOREAL PREDATORY FISH SPECIES

2.1 Introduction

Mercury is a pervasive neurotoxin, known to pose risks to the health of humans and wildlife (NRC 2000, Mergler et al. 2007). It is one of the most widespread contaminants in fish, and the primary contaminant of concern in Ontario's Boreal Shield lakes (MOECC 2016). Mercury toxicity is dependent on speciation and exposure pathway. In freshwater, mercury is found in three forms: elemental (Hg°), inorganic (Hg(II)) and its most toxic state, organic methylmercury (MeHg(I)). Both inorganic and organic mercury bioaccumulate in biota; however, the uptake rate and tissue retention of Hg(II) is poor relative to MeHg(I) (Mason et al. 1995; Trudel and Rasmussen 1997). While most of the mercury detected in the water is inorganic, 95%-100% of the total mercury concentration ([THg]; sum of all Hg forms) in adult fish tissue is in the organic MeHg(I) form (Grieb et al. 1990, Bloom 1992, Loux 1998). Methylmercury is easily absorbed and biomagnifies in aquatic food webs, with highest MeHg(I) concentrations in top aquatic predators (Ratkowsky et al. 1975; Cabana et al. 1994; Kidd et al. 1995). Due to its strong affinity for thiol groups (Lemes and Wang 2009), the bulk of bioaccumulated MeHg(I) is stored in fish muscle tissue (Boudou and Ribeyre 1983), resulting in human exposure to MeHg(I) and the issuance of many fish consumption advisories worldwide (Evers et al. 2014).

In Boreal Shield lakes, mercury arrives via atmospheric deposition (mainly wet precipitation) and indirectly through the watershed (e.g. terrestrial runoff) (Rudd 1995,

Fitzgerald et al. 1998, Lockhart et al. 1998). In most Ontario Boreal Shield lakes, atmospheric deposition is generally thought to be the leading source of mercury input (Lockhart et al. 1998), however, the relative contributions of mercury falling directly on the lake surface vs mercury arriving indirectly via the watershed are lake specific (Harris et al. 2007). Experimental mesocosm and whole lake studies have shown a strong relationship between atmospheric deposition of mercury and MeHg(I) in fish tissue (Downs et al. 1998, Hammerschmidt and Fitzgerald 2006, Harris et al. 2007, Orihel et al. 2007). Directly adding a measured concentration of mercury to a system leads to a linear increase in MeHg(I) concentration in biota. If mercury in fish is tightly coupled to atmospheric deposition, then one would expect fish tissue mercury levels to decline with a reduction in atmospheric mercury deposition.

In North America, mercury emissions have drastically declined since the 1980s (Schuster et al. 2002; Prestbo and Gay 2009; Pacyna et al. 2010), and are forecasted to drop even lower (UNEP 2013), but fish mercury concentrations in Boreal Shield lakes of Ontario have not shown a similar trend, and appear to be rising in some areas (Tang et al. 2013; Gandhi et al. 2014;Chen et al. 2018). Mercury cycling is complex (Morel et al. 1998), and despite lowered emissions and deposition rates within North America, historical mercury loadings are still present in the environment; stored in soils, wetlands, and lake sediments (Bindler et al. 2001, Harris et al. 2007, Muir et al. 2009). Additionally, as mercury emissions decline in North America, they continue to rise in other parts of the world (UNEP 2013). Due to mercury's long residence time in the atmosphere (Fitzgerald and Mason 1997), emissions from Asian countries, where Hg emissions are on the rise, may then be dispersed around the earth prior to deposition.

Therefore, current global emissions, and perhaps continued release of historically deposited mercury, may very well be contributing to the lack of decline, or rise, in fish mercury levels in Ontario's Boreal Shield. Given this persistent mercury problem, it is important that we broaden our understanding of the factors that influence these concentrations at various spatio-temporal scales. In general, these factors can be divided into two major categories: (1) those influencing the rate of production of MeHg(I), and (2) those influencing the rates of MeHg(I) uptake, retention, and movement through the food web to fish.

Conversion of total Hg to MeHg(I) in boreal aquatic systems is primarily carried out by sulfate-reducing bacteria, and conditions that favour these microbes tend to favour methylation (Ullrich et al. 2001; Lehnherr 2014). Methylmercury production is influenced by the availability of inorganic Hg(II), but has also been linked to many other environmental factors. Temperature (Bodaly et al. 1993), dissolved oxygen (Eckley and Hintelmann 2006), pH (Miskimmin et al. 1992), dissolved organic carbon (Watras et al. 1998), availability of sulphate (Gilmour et al. 1992), watershed catchment size (Schindler et al. 1995) , and macrophyte type and abundance (Guimaraes et al. 2000) may all influence methylation and/or demethylation rates within lakes, and hence the net MeHg(I) production. Variability in fish [THg] among boreal lakes is often most strongly related to the physical-chemical factors that are known to influence MeHg(I) production (McMurtry et al. 1989, Sumner 2016). However, if all fish within a system are exposed to the same environmental conditions, and presumably similar base levels of mercury, what may be more relevant than the rate of MeHg(I) production in understanding among

species variability in [THg], would be factors directly, or indirectly, influencing the movement of MeHg(I) (e.g. fish physiology and food web structure).

Mercury concentrations in fish typically increase with overall body size and age (Grieb et al. 1990; Somers and Jackson 1993; Sonesten 2003). As fish grow in size, and their gapes become larger, their capacity to feed on larger, and potentially more-contaminated prey, also increases. Mercury bioaccumulates when the rate of absorption exceeds the rate of excretion (Trudel and Rasmussen 2006). Older and larger fish must be feeding on prey with elevated mercury concentrations in order for mercury to remain correlated with age and size (Trudel and Rasmussen 2006). This, however, is not always the case; despite feeding on larger prey, some studies have indeed found that fish mercury concentrations in some populations are not always correlated with size and age (Scott and Armstrong 1972; Meili 1991), suggesting that exposure alone cannot explain all temporal variability in [THg] bioaccumulation in fish. Other physiological mechanisms related to growth are necessary to help explain observed differences in fish [THg] (Trudel and Rasmussen 2006). While growth is strongly related to factors that influence the bioaccumulation of mercury in fish, the effects of somatic growth rate (increase in body size over time) on mercury bioaccumulation appears to vary. Various studies have found no correlation (Stafford and Haines 2001), positive correlations (Dutton 1997), and negative correlations (Schindler et al. 1995, Simoneau et al. 2005, Ward et al. 2010) between mercury concentrations and fish growth rates. The bulk of the literature, however, supports a negative relationship between MeHg(I) concentrations in muscle tissue and growth rate due to greater biomass gains relative to MeHg(I) gains in faster-growing fish (Doyon et al. 1998; Karimi et al. 2007).

The structure and composition of a fish's food web also plays a leading role in influencing the uptake of MeHg(I). More than 90% of an adult fish's MeHg(I) exposure comes from food rather than directly through water (Hall et al. 1997). Knowing what a fish eats and where it is feeding is therefore pivotal to understanding THg concentrations in fish tissues. Stable isotope ratios of carbon ($^{13}C/^{12}C$; $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) can be used to assess mercury transfer through the food web (Power et al. 2002). As described in Chapter 1, some vertical energy transfers can be traced using $\delta^{13}C$. However, due to the complexity of food webs and the energy fluxes that exist across habitats (Vadeboncoeur et al. 2002), $\delta^{13}C$ is not always the most reliable global indicator of mercury transfer. Fish tissue mercury has been linked to both pelagic and benthic sources of carbon, but the pathways of mercury movement clearly differ from one system to the next (Power et al. 2002, Gorski et al. 2003, Eagles-Smith et al. 2008, Kidd et al. 2012, Lescord et al. 2015). Nevertheless, carbon isotopes remain useful in determining the primary production source of a fish's diet, and ultimately where mercury is first being introduced into the food web. In contrast to the challenges with carbon isotopes, numerous studies have found a clear and positive correlation between fish mercury concentrations and $\delta^{15}N$ (Kidd et al. 1995; Eagles-Smith et al. 2008), with evidence of enrichment of $\delta^{15}N$ with each successive step in the food web. Nitrogen isotopic ratios have thus proven to be very useful for predicting potential trophic mercury transfers in fish.

The objective of my study was to compare the relative importance of trophic position (inferred from $\delta^{15}N$), energy source (inferred from $\delta^{13}C$), and growth rate (lifetime growth rate, LGR, $g \cdot year^{-1}$) in accounting for interspecific variation in muscle

mercury concentrations for co-occurring piscivores in boreal lakes. Because of the numerous abiotic and biotic factors which promote mercury methylation in lakes, I hypothesized that fish muscle mercury concentrations would vary predominantly at the ecosystem level (i.e., among lakes; Kamman et al. 2005, Depew et al. 2013). Given that > 90% of MeHg(I) exposure comes from diet, and relative to growth rate, $\delta^{15}N$ has been a more reliable predictor of [THg] in adult fish, I also hypothesized that variability in [THg] among piscivores would be more strongly related to differences in their food web positions than differences in their growth rates.

To meet my objective and test my hypotheses, I sampled fish from Ontario lakes with co-habiting populations of northern pike (*Esox lucius*), walleye (*Sander vitreus*), burbot (*Lota lota*) and lake trout (*Salvelinus namaycush*). This unique, balanced design allowed me to account for among-lake variation while examining interspecific variation. Subsequently, I modeled the muscle [THg] of these four species with respect to trophic position, energy source, and somatic growth rate to determine which combination of these predictors would best explain the observed variability un-accounted for by differences in ecosystems.

2.2 Methods

Sampling and parameter selection

As described in Chapter 1, the same 27 Ontario Boreal Shield study lakes (Fig. 1.2 and Table 1.2) and four predatory species (lake trout, northern pike, walleye and burbot) were sampled to explore drivers of interspecific mercury variability among co-occurring predators. The selected study lakes had no known point sources of mercury, and it is assumed that all direct mercury inputs were from atmospheric deposition and indirect

inputs from watershed runoff. Procedures for sampling fish, and collection of attribute data and tissue samples were analogous to those reported in Chapter 1, the only variant being, after sub-sampling the frozen axial muscle tissue for stable isotope analyses, the remainder of the frozen muscle tissue was used for mercury analysis. Methods for stable isotope analysis are outlined in Chapter 1. While a minimum of 10 samples were collected per species per lake, the total number of samples analysed for various parameters ([THg], age and stable isotopes) varied among populations. A summary of total sample sizes by population for ages and stable isotopes is presented in Appendix A (Table A1), and species-specific sample sizes for [THg] are presented in Table 2.1 in the results section of this chapter.

Mercury analysis of muscle samples was carried out by the Ontario Ministry of the Environment and Climate Change (MOECC) Laboratory Services Division (Etobicoke, ON). Total mercury concentrations ([THg]) were determined by cold vapour flameless atomic absorption spectroscopy (CVFAAS) following MOECC protocol E3057A, and values were reported in micrograms per gram of wet tissue ($ug \bullet g^{-1}$ or ppm). Samples were not analyzed for MeHg(I) specifically since more than 95% of the THg in adult predatory fish is MeHg(I) (Bloom 1992), and laboratory methods for [THg] determinations are simpler and less expensive than those for [MeHg].

All fish were aged using standard protocols (Mann 2017). Over 95% of the collected fish ageing structures were analyzed by a single reader at the MNRF Northwest Ageing Lab (Dryden, ON). Ages for the remaining structures were determined either by an external service lab (Northshore Environmental, Thunder Bay, ON), or in-house by trained students at the Cooperative Freshwater Ecology Unit (Laurentian University,

Sudbury, ON). Whole cleithra were used for ageing northern pike, and sagittal otoliths were used for ageing the other three species. Walleye and burbot otoliths were prepared following the 'crack-and-burn' method which consists of splitting the otolith with a scalpel across the transverse plane and lightly burning the broken surface to make the annuli more distinct. Lake trout otoliths were prepared using the 'section-and-polish' method, which involves cutting a thin transverse section (perpendicular to longitudinal axis) through the nucleus with a jeweller's saw, mounting the section onto a microscope slide and polishing it with fine abrasive paper until the annuli become more distinct. Ages were determined by counting annuli on whole cleithra, and the burned or polished otolith surfaces by observing them under a dissecting scope using reflected light. I estimated individual lifetime growth rate for each fish by dividing fish body weight by age (LGR, $g \bullet year^{-1}$). This method for calculating fish growth allowed me to determine the average increase in fish body mass from birth to the time of capture for all populations regardless of sample size.

Data handling and analysis

All analyses were performed using the statistical computing package R 3.4.0 (R Core Team 2017). Data were rigorously scrubbed to detect potential outliers and possible influential data points. Linearized relationships between fish weight (RWT) and total length (TL), LGR, [THg], $\delta^{15}N$ and $\delta^{13}C$ were examined at a population level (species by lake). Obvious outliers were further investigated, and all identified data points with both a studentized residual greater than 3 and a Cook's distance greater than the cut off (4/(n-k-1); n = sample size, k = number of independent variables) (Fox 1997), were either corrected for human error or removed. Less than 1% of data were removed.

Previous studies have shown that both my response variable, muscle [THg], and my predictors, $\delta^{15}N$ and growth rate, can be correlated with fish body size (Romanuk et al. 2011, Depew et al. 2013). In Chapter 1, I also observed $\delta^{13}C$ to be correlated with body size for certain populations (Fig. 1.3). Thus, in order to examine the relative effects of these predictors on muscle [THg], I had to account for possible covariation. I used an ANCOVA approach to calculate least squares adjusted mean values of [THg], $\delta^{15}N$, $\delta^{13}C$ and LGR at a standard fish body mass of 1 kg for each population. Because of interspecific variation in body shapes, mass was considered a better metric of body size than length for making among-species inferences. These population means, adjusted to 1 kg, were used in all subsequent analyses. To identify the degree to which species varied in [THg], food web position ($\delta^{15}N$ vs $\delta^{13}C$) and LGR, the mean size-adjusted values were plotted by species, and all taxonomic pairs were compared using Tukey's HSD tests.

Like all studies which utilize $\delta^{15}N$ and $\delta^{13}C$ to make inferences about trophic position and energy pathways in food webs, I had to consider the likely occurrence of fluctuating baseline isotope ratios across my 27 study lakes. Baseline correction methods employed in the literature are variable depending on the goal of the study. For nitrogen, a common and widely applied method is to calculate the trophic position (TP) of an organism using the following equation (Vander Zanden and Rasmussen, 1999):

$$(1) \quad TP_{fish} = [\frac{(\delta^{15}N_{fish} - \delta^{15}N_{baseline})}{\Delta 15N}] + \lambda$$

where $\delta^{15}N_{baseline}$ is the measured $\delta^{15}N$ of a primary producer or consumer species, $\Delta 15N$ is the trophic enrichment factor (TEF), often a value between 2 and 5‰ (Post 2002), and λ is the trophic position of the organism used to estimate $\delta^{15}N_{baseline}$ (e.g., λ = 1 for

primary producer and 2 for primary consumer). When consumers rely on more than one food web, mixing-models are used to calculate trophic position (Post 2002). Other studies have simply adjusted their consumer $\delta^{15}N$ by subtracting mean baseline $\delta^{15}N$ measures of basal organisms from the same lake (Lescord et al. 2015):

(2) $$\delta^{15}N_{adjusted} = \delta^{15}N_{fish} - \delta^{15}N_{baseline}$$

For carbon, methods for baseline correction are not as rigid. As discussed in Chapter 1, carbon fractionation across trophic levels is low, thus big differences between basal and consumer carbon values were not expected. However, baseline carbon signatures may still vary among lakes due to unique proportions of carbon inputs into each lake (i.e., proportion of allochtonous vs autochtonous carbon). Therefore, consumer carbon values should also be adjusted to reflect lake-specific baseline signatures. One way of adjusting carbon values is by calculating the proportion of pelagic or benthic carbon in a consumer using a two end-member mixing model to estimate a consumer's fractional reliance on either benthic or pelagic prey (Vander Zanden and Rasmussen 2001):

(3) $$\%_{\text{benthic}} = [(\delta^{13}C_{fish} - \delta^{13}C_{pelagic})/(\delta^{13}C_{benthic} - \delta^{13}C_{pelagic})] \bullet 100$$

where $\delta^{13}C_{pelagic}$ is the mean pelagic source (e.g.. phytoplankton or unionid mussels) and the $\delta^{13}C_{benthic}$ is the mean benthic source (e.g., periphyton or snails). Unionid mussels and snails are two of the most commonly used taxa for estimating baseline $\delta^{15}N$ and $\delta^{13}C$ in boreal lakes. While mussels and snails were collected from some of my study lakes, I only had sufficient sample sizes of these baseline organisms from 7 of 27 lakes, thus I employed a different method to account for baseline variation in $\delta^{15}N$ and $\delta^{13}C$ among

lakes. Using a one-way ANOVA, I modeled the relationship between the size-adjusted isotopic values for fish (dependent variables; $\delta^{15}N$ and $\delta^{13}C$) and the class variable "lake" (independent variable). I computed the residuals for each model and used them in place of traditional baseline-adjusted values for all subsequent analyses which effectively removed the "lake effect" from the isotope data. The residuals method has not been commonly used in the isotope world (Swanson and Kidd 2010), but has been employed in toxicology studies to correct for differences in background concentrations of various contaminants (Cabana et al. 1994; Richardson and Currie 1995; Donoghue et al. 1998).

To validate the method, I calculated adjusted $\delta^{15}N$ ($\delta^{15}N_{adjusted}$, eqn. 2) and percent benthic carbon (PB, eqn. 3) of all four species, for the 7 lakes for which I had isotope data for baseline organisms. I examined the relationships between $\delta^{15}N_{adjusted}$ and the computed residuals for $\delta^{15}N$, and between PB and the $\delta^{13}C$ residuals. These relationships were linear across lakes, and overall were quite strong (R^2 = 0.71 and 0.51; Figs. 2.1 and 2.2). As such, I used the residuals method in place of traditional baseline-adjustment methods. In addition to lake-standardizing the size-adjusted $\delta^{15}N$ and $\delta^{13}C$ values, I also adjusted LGR and [THg] to account for the inherent differences in fish growth and background mercury levels among lakes.

Using the computed residuals and scatterplot matrices, I ran Spearman correlations to examine the relationships between [THg] and the predictor variables ($\delta^{15}N$, $\delta^{13}C$ and LGR) for a 1 kg fish of each species across lakes. Because the strengths of the correlations were variable among species, I constructed a series of candidate linear mixed effects models (LMEM) relating the size-adjusted population means of [THg] to the residuals of the size-adjusted population means of $\delta^{15}N$, $\delta^{13}C$ and LGR as fixed

continuous effects. The residual values in all candidate models were scaled and centered to generate standardized coefficients (Schielzeth 2010, Grueber et al. 2011). Each model included lake as a categorical random effect to account for variation in [THg] attributed to overall differences in ecosystems (random intercept). I also included species as a random effect (slope only) to account for varying slopes between the response variable ([THg]) and the individual predictor variables ($\delta^{15}N$, $\delta^{13}C$ and LGR). This allowed me to further tease apart the variation in [THg] which was attributed to, not only differences among environments, but overall differences among species and more specifically differences due to $\delta^{15}N$, $\delta^{13}C$ and LGR. Seven models were constructed using all possible combinations of the predictor variables as fixed effects. I constructed two additional models, the first related size-adjusted population means of [THg] to the categorical fixed effect of species, with lake as a random effect. This model was used to look specifically at what proportion of mercury variability was explained solely by differences among predators. The second was an intercept model that included only lake as a random effect which allowed me to quantify how much of the variation in mercury was due to differences in lakes alone.

I used an information theoretic approach to assess the relative importance of the three predictor variables ($\delta^{15}N$, $\delta^{13}C$ and LGR), relative to one another, in explaining the variation in fish [THg]. All nine models were ranked using a Second-Order Information Criterion (AIC_c). In addition to model ranking using AIC_c, I also computed the conditional and marginal R^2 values to help address questions related to strength of evidence, and to quantify variance in [THg] attributed to different fixed and random effects. The conditional R^2 describes the proportion of variance explained by the entire

model, fixed and random effects inclusive. The marginal R^2 describes the proportion of variance explained solely by the fixed effects. The R^2 values, however, are not thought to be useful in model selection (McQuarrie and Tsai 1998; Burnham and Anderson 2002).

To test the robustness of my results, models were also fitted and ranked using smaller subsets of the lakes, and slightly different methods. First, models were built using traditional baseline-corrected values for $\delta^{15}N$ ($\delta^{15}N_{adjusted}$, eqn. 2) and $\delta^{13}C$ (PB, eqn. 3), and compared to the residual method for the 7 lakes for which I had baseline data. Second, models were built using population mean values of [THg], LGR, $\delta^{15}N$ and $\delta^{13}C$ adjusted to standard masses of 0.5 kg (n = 13 lakes) and 1500 g (n = 21 lakes).

All AIC_c model ranking and R^2 estimates were completed using R packages lme4 (Bates et al. 2015), AICcmodavg (Mazerolle 2017) and MuMIN (Bartoń 2018).

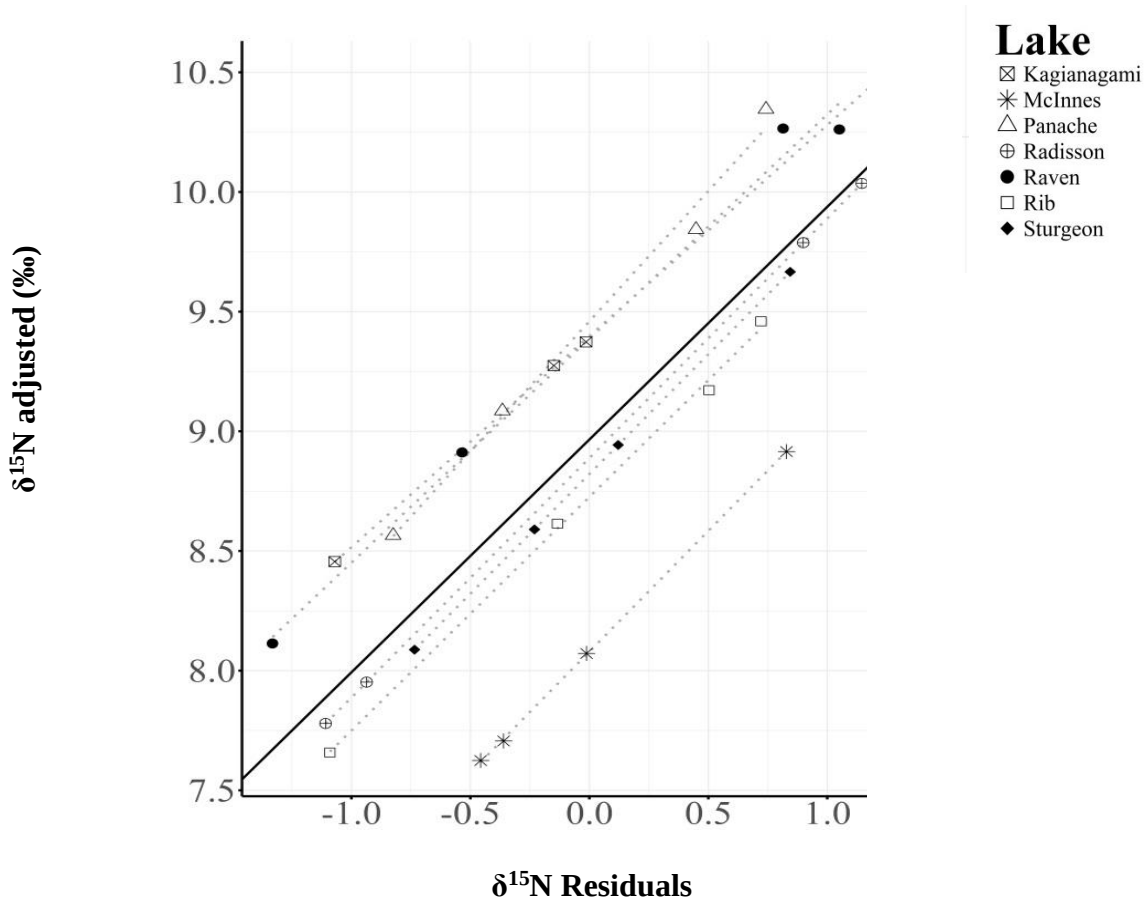

Figure 2.1 Linear relationships plotted between the corrected baseline values of $\delta^{15}N$, calculated using the traditional method ($\delta^{15}N_{adjusted}$, eqn. 2), vs. the computed residuals used to lake-standardize $\delta^{15}N$ for four size-adjusted (1 kg) fish species (burbot, lake trout, northern pike and walleye). n = 7 lakes.

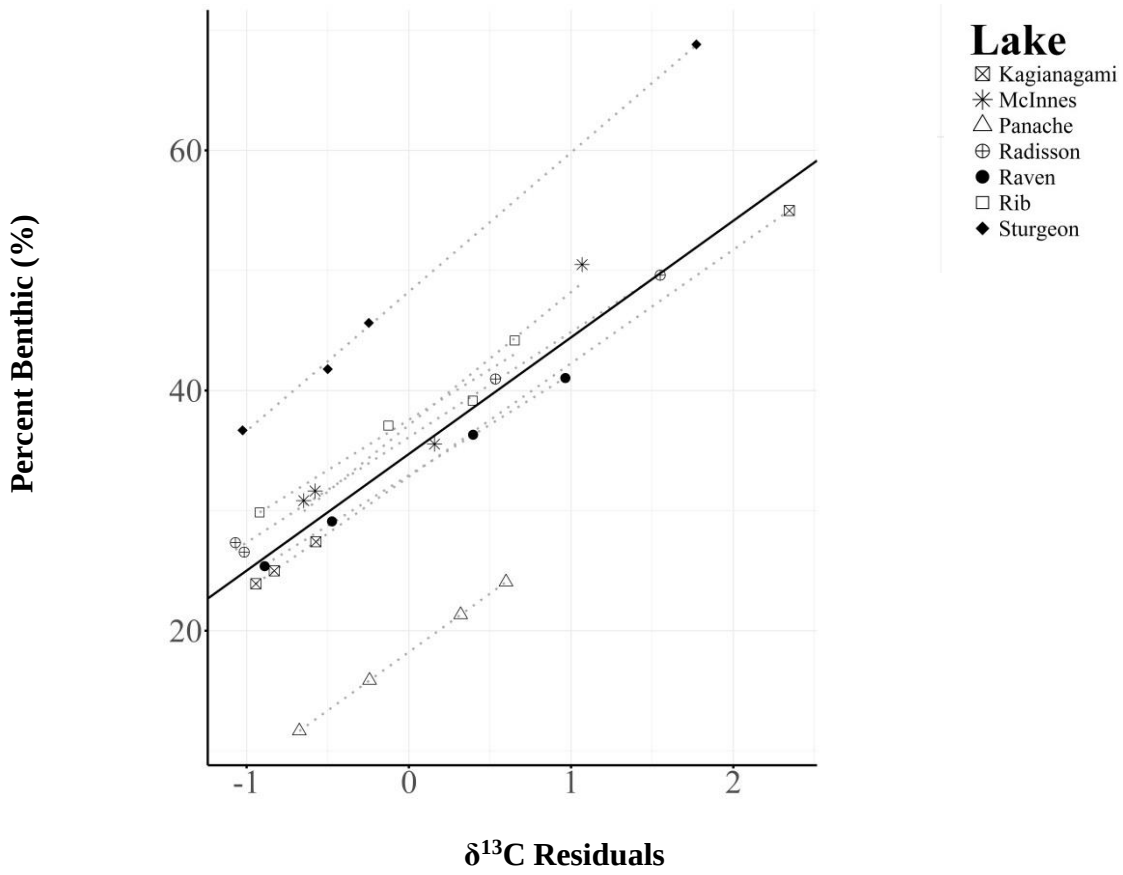

Figure 2.2 Linear relationships plotted between the corrected baseline values of $\delta^{13}C$, calculated using two end-member mixing model (PB, eqn. 3) vs. the computed residuals used to lake-standardize $\delta^{13}C$ for four size-adjusted (1 kg) fish species (burbot, lake trout, northern pike and walleye). n = 7 lakes.

2.3 Results

Summary of among-species variability for [THg] and predictor variables

Prior to adjusting [THg] values to a standard body size of 1 kg, the largest fish sampled were lake trout and northern pike, and the smallest were walleye and burbot. Despite the high maximum body weight of collected individuals, northern pike had lower maximum and mean [THg] relative to walleye (Table 2.1). Overall, within species variation of [THg] was lowest in burbot relative to the other three study species. Stable isotope values and fish ages are presented in Appendix A (Table A1).

Mean [THg] for a 1 kg fish was greatest in burbot and lowest in northern pike (Fig. 2.3a). Mean [THg] did not differ between burbot and walleye ($p = 0.64$) or lake trout and northern pike ($p = 0.25$). However, mean [THg] values were significantly different in all other pairwise contrasts ($p < 0.05$; Fig. 2.3). Intraspecifically, burbot and walleye populations exhibited the largest variability in mean [THg]; values ranged from 0.25 to 1.57 ppm, and 0.27 to 1.10 ppm, respectively. Lake trout and northern pike mean [THg] were less variable among populations and ranged from 0.24 to 0.85 ppm and 0.15 to 0.86 ppm, respectively.

Growth rates were variable among the four study species (Fig. 2.3b). Northern pike was the fastest growing and burbot the slowest. At 1 kg, northern pike, walleye and burbot exhibited significantly different mean LGR ($p < 0.001$) relative to one another (Fig. 2.3b). Lake trout appeared to grow at a similar rate to burbot ($p = 0.71$), but significantly slower than walleye and northern pike ($p < 0.001$; Fig. 2.3b). The greatest variability in mean growth rates among populations was observed in lake trout and in northern pike. At 1 kg, LGR in lake trout ranged from 39.6 to 278 $g \cdot year^{-1}$, and in

northern pike, from 184 to 426 g·year^{-1}. Of the four species, intraspecific variability in LGR was smallest in burbot, ranging from 37.6 to 168 g·year^{-1}.

Food web positions were polarized (Fig. 2.3c). Lake trout and burbot had a mean $\delta^{15}N$ value of 10.87 ‰, and occupied higher trophic positions than walleye and northern pike ($p < 0.001$). Walleye occupied a slightly higher trophic position than northern pike (Fig. 2.3c); however, the mean adjusted $\delta^{15}N$ values were not statistically different. With the exception of burbot and walleye, which appear to share identical sources of carbon (mean $\delta^{13}C$ = -26.30 ‰), all pairwise comparisons of $\delta^{13}C$ indicated that energy sources differed among species ($p < 0.05$); lake trout were more distinctly pelagic compared to burbot, walleye and northern pike.

Correlative relationships between [THg] and predictor variables

Using the population adjusted residuals for a 1 kg fish, I ran a Spearman correlation analysis to assess possible covariation between [THg], LGR, $\delta^{15}N$ and $\delta^{13}C$ for all four study species. The most consistent trends observed were the positive relationship between [THg] and $\delta^{15}N$, and the negative relationship between [THg] and LGR (Table 2.2). All species, with the exception of lake trout, showed significant, moderate to strong correlations between [THg] and $\delta^{15}N$ (Table 2.2). Correlation between [THg] and LGR was moderate to strong for all species except northern pike (Table 2.2). [THg] in walleye was more closely correlated with LGR than $\delta^{15}N$ (Table 2.2), and [THg] in burbot was only slightly more correlated to $\delta^{15}N$ than LGR (Table 2.2). However, LGR and $\delta^{15}N$ for both walleye and burbot were strongly related (Table 2.2) suggesting potential species-specific covaried effects on [THg]. In contrast to LGR and $\delta^{15}N$, carbon values were not significantly correlated with any variable. In northern pike,

[THg] and $\delta^{13}C$ were negatively associated (Table 2.2), while in lake trout the trend was positive (Table 2.2), but neither of these correlations were significant.

AIC_c model ranking

Of the nine candidate LMEMs constructed, the four top-ranked models all included $\delta^{15}N$ as a predictor (Table 2.3). The standardized coefficients for LGR, however, were all larger than those of $\delta^{15}N$ (Table 2.3). The model with LGR and $\delta^{15}N$ as the only two predictors of [THg] was the model which ranked highest, and the model which ranked second included $\delta^{15}N$ as the sole predictor of [THg] (Table 2.3). The evidence ratio of 1.8 (w_1/w_2) measured between the top-ranked model and the second indicates weak support for the top model, and the likelihood of it being better than its successor is poor. Models ranked third and fourth had moderate support ($\Delta_i < 5$, wi = 0.1), while the remaining models had little to no support ($\Delta_i > 17$, wi = 0.0) (Anderson 2008). Despite the low Δ_i and w_i values, the model with both $\delta^{15}N$ and $\delta^{13}C$ ranked fourth, and above the model with LGR alone.

Variance in mean muscle [THg] explained by the fixed effects only was very low for all reported models (R^2_{marg} = 0.08 to 0.15, Table 2.3). The conditional R^2 values, however, were moderate to high across all models (R^2_{cond} = 0.44 to 0.80; Table 2.3) indicating that the random effects (lake and species) accounted for most of the observed variance in muscle [THg]. The null model with lake as a random intercept (lake effect) accounted for 44% of the total variance in [THg]. Adding species as a fixed effect to this base model accounted for 15% of the remaining unexplained variance (R^2_{marg} = 0.15; Table 2.3). For the 15% of variance in [THg] explained by overall species differences,

approximately half (6 - 8%) could be attributed specifically to differences in food web position and/or species-specific growth rates (Table 2.3).

Regardless of the standard adult body size selected (500 g, 1000 g or 1500 g), or the baseline correction method used (traditional or residual), lake accounted for the greatest percentage of explained variance in muscle [THg]. $\delta^{15}N$ was the leading predictor of variance in muscle [THg] among 500 g and 1500 g burbot, lake trout, northern pike and walleye. Both model-ranking analyses used to compare baseline correction methods (n = 7 lakes) suggested that LGR was the strongest predictor of [THg]. The complete AIC_c tables for the alternate model-ranking analyses are reported in Appendix B (see Tables B1, B2, B3 and B4).

Table 2.1 Summary of means and ranges of fish weights (g), and means (± 1 SD) and ranges of muscle total mercury concentrations ([THg], ppm wet) prior to size standardizing to 1 kg. Sample sizes represent pooled numbers across all 27 study lakes.

Species	Sample size (n)	Mean Weight (g)	Weight Range (g)	Mean [THg] (ppm, wet)	Range [THg] (ppm, wet)
Burbot	615	745.70	35 - 3,329	0.51 ± 0.29	0.06 - 1.80
Lake trout	687	1647.62	14 - 14,706	0.64 ± 0.52	0.04 - 4.90
Northern pike	553	1633.69	28 - 9,805	0.59 ± 0.47	0.03 - 2.80
Walleye	794	732.80	17 - 5,600	0.64 ± 0.50	0.07 – 5.10

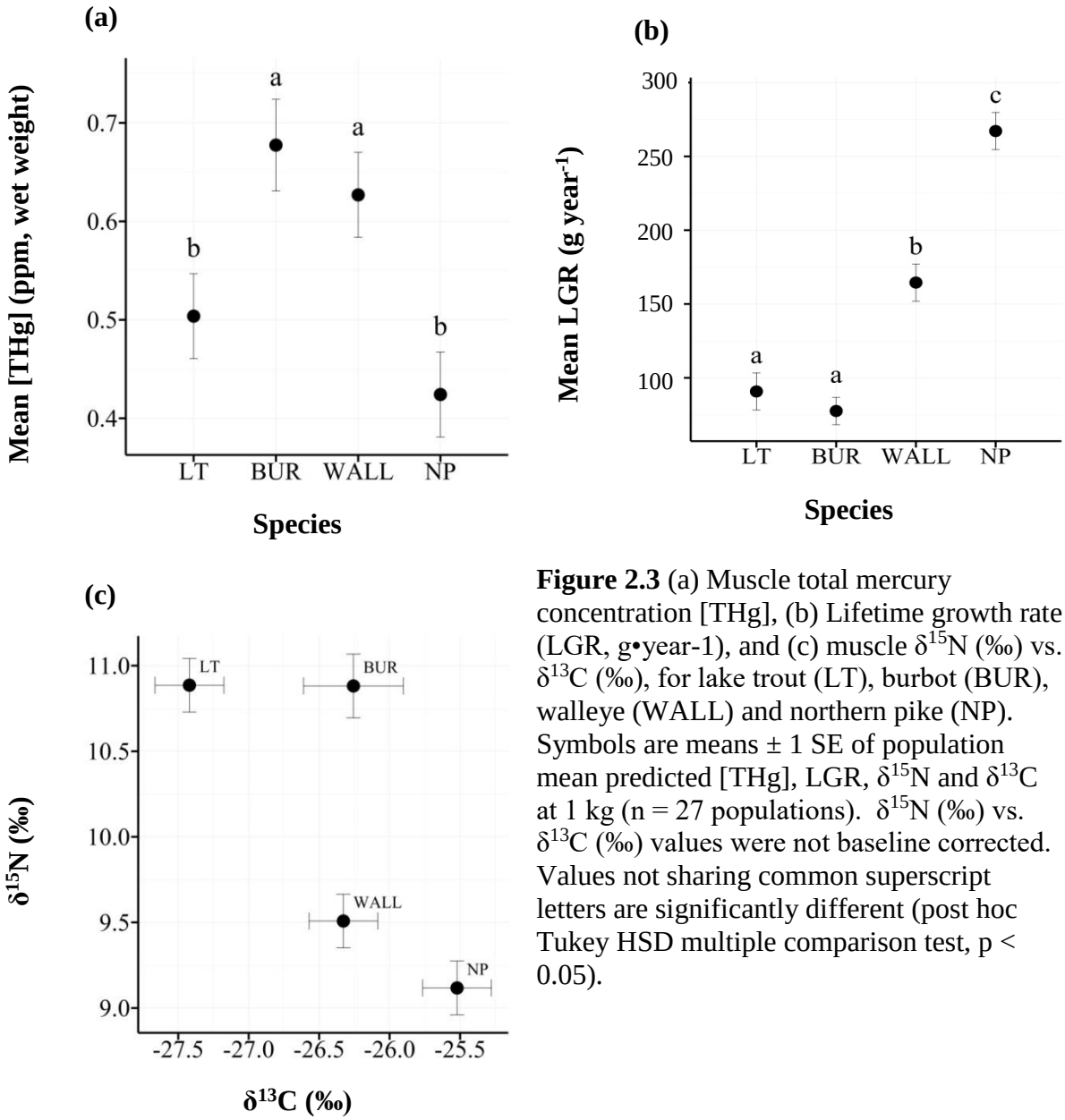

Figure 2.3 (a) Muscle total mercury concentration [THg], (b) Lifetime growth rate (LGR, g•year-1), and (c) muscle $\delta^{15}N$ (‰) vs. $\delta^{13}C$ (‰), for lake trout (LT), burbot (BUR), walleye (WALL) and northern pike (NP). Symbols are means ± 1 SE of population mean predicted [THg], LGR, $\delta^{15}N$ and $\delta^{13}C$ at 1 kg (n = 27 populations). $\delta^{15}N$ (‰) vs. $\delta^{13}C$ (‰) values were not baseline corrected. Values not sharing common superscript letters are significantly different (post hoc Tukey HSD multiple comparison test, $p < 0.05$).

Table 2.2 Spearman correlation matrices for 1 kg adjusted population mean residuals of muscle total mercury concentration ([THg]; ppm wet), lifetime growth rate (LGR; g•year^{-1}), muscle $\delta^{15}N$ (‰) and muscle $\delta^{13}C$ (‰) for burbot, lake trout, northern pike and walleye. Correlation coefficients (r) are presented and significant correlations are indicated: *p<0.05, **p<0.01, ***p<0.001. Sample size, n = 27 lakes.

Burbot				
	Hg	**LGR**	**$\delta^{15}N$**	**$\delta^{13}C$**
Hg	1			
LGR	**-0.61 *****	1		
$\delta^{15}N$	**0.68 *****	**-0.53 ****	1	
$\delta^{13}C$	0.07	-0.17	0.18	1
Lake Trout				
Hg	1			
LGR	**-0.48 ***	1		
$\delta^{15}N$	0.14	0.25	1	
$\delta^{13}C$	0.31	-0.06	-0.11	1
Northern Pike				
Hg	1			
LGR	-0.3	1		
$\delta^{15}N$	**0.53 ****	-0.12	1	
$\delta^{13}C$	-0.33	0	-0.15	1
Walleye				
Hg	1			
LGR	**-0.65 *****	1		
$\delta^{15}N$	**0.47 ***	**-0.67 *****	1	
$\delta^{13}C$	-0.03	0.16	-0.07	1

Table 2.3 Summary of nine models ranked by second order Akaike Information Criterion (AIC_c) relating mean muscle total mercury concentration in a 1 kg fish to Species (class variable), trophic position ($\delta^{15}N$), energy source ($\delta^{13}C$), and lifetime growth rate (LGR). Each model had a random effect term specified by Lake (random intercept), and all models, except the species fixed effects model, also included a random slope term representing species (random slope). K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights (%), R^2_{Marg} = marginal R^2 and R^2_{Cond} = conditional R^2.

Fixed Effects and Standardized Coefficients	**Rank**	**K**	**AIC_c**	**Δ_i**	**w_i**	**R^2_{Marg}**	**R^2_{Cond}**
$\delta^{15}N$ (0.02), LGR (-0.06)	1	7	-53.9	0	0.56	0.08	0.80
$\delta^{15}N$ (0.06)	2	5	-52.72	1.18	0.31	0.05	0.72
$\delta^{15}N$ (0.03), LGR (-0.05), $\delta^{13}C$ (0.01)	3	9	-49.69	4.21	0.07	0.08	0.80
$\delta^{15}N$ (0.07), $\delta^{13}C$ (0.01)	4	7	-49.48	4.41	0.06	0.06	0.72
LGR (-0.09), $\delta^{13}C$ (0.03)	5	7	-36.53	17.37	0.00	0.10	0.67
LGR (-0.07)	6	5	-36.2	17.7	0.00	0.08	0.67
Species	7	6	-32.95	20.95	0.00	0.15	0.64
$\delta^{13}C$ (0.02)	8	5	-15.09	38.8	0.00	0.00	0.58
Intercept	9	3	-4.06	49.84	0.00	0.00	0.44

2.4 Discussion

Several earlier studies have also attempted to identify the drivers of interspecific variability in mercury concentrations in freshwater fish assemblages (McGill et al. 2006, Swanson et al. 2006, McIntyre and Beauchamp 2007, Donald et al. 2015); however, to my knowledge this is the first study to examine a piscivore assemblage with comparable sample sizes for burbot, lake trout, northern pike and walleye. Donald et al. (2015) assessed the relationships between muscle [THg] and age, mass, body condition, $\delta^{15}N$ and $\delta^{13}C$ for a functional group of piscivores comprised of northern pike, walleye, and sauger (*Sander canadensis*) from Lake Diefenbaker, Saskatchewan. They grouped all the predators together allowing them to explore predictors of mercury across piscivores, but did not explore how [THg] varied among the three species. Swanson et al. (2006) did standardize muscle [THg] to a common body size and included growth rate as a predictor variable, but examined small-bodied, forage fish communities. Simoneau et al. (2005) examined how growth rate could modulate and explain [THg] variability, but only intraspecifically across 12 populations of walleye, and did not distinguish the waterbody effect from the growth effect. All of these earlier studies came to slightly different conclusions, but all agreed that the best predictors of mercury, whether it was growth rate (Simoneau et al. 2005, Swanson et al. 2006) or food web position (Donald et al. 2015), could only explain a small portion of the observed variability in intra- and interspecific [THg]. Additionally, none of the aforementioned studies teased apart variation in [THg] attributed to differences in waterbodies as well as species-specific variation in [THg].

As hypothesized, most of the variability in fish [THg] observed across my 27-lake data set was attributable to ecosystem-level differences. Lake alone accounted for 45% of

the variance in muscle [THg]. Fish mercury concentrations are expected to vary between ecosystems as lake-specific mercury methylation and demethylation rates influence net MeHg production, and waterborne [MeHg]. However, the degree to which muscle [THg] varied interspecifically, and how the remaining variance partitioned among predictors following removal of the lake effect, was interesting given that all four study species are presumed to be predominantly piscivorous (Chapter 1).

Among species variability

Muscle [THg] among the four co-occurring species was divided into two groups; burbot and walleye had similar and relatively higher muscle [THg], whereas lake trout and northern pike had similar and relatively lower muscle [THg]. This was surprising given that these two pairings of fish are ecologically distinct (see Fig. 1.1 and Table 1.1 in Chapter 1). Although most earlier studies did not standardize to 1 kg, previous findings have also found muscle [THg] to be greater in walleye than in northern pike and lake trout (Mathers and Johansen 1985, Kidd et al. 1995, Kamman et al. 2005, Lockhart et al. 2005, Depew et al. 2013, Donald et al. 2015). The high size-standardized mean [THg] observed in burbot and low [THg] in northern pike, however, was not expected. Earlier studies have found burbot to have lower [THg] compared to lake trout and northern pike (Kidd et al. 1995) and lower mercury uptake rates relative to lake trout (Power et al. 2002); and northern pike generally have higher [THg] compared to burbot and lake trout (Kidd et al. 1995, Kamman et al. 2005). The differences in interspecific variation observed in fish muscle [THg] between my study and those reported in the literature could be attributed to (1) small sample sizes, (2) the inconsistent size/age standardization of [THg] values, or (3) confounding waterbody and species effects. In my raw data, prior

to size standardizing, I also observed lower mean [THg] in burbot relative to all other species. However, my overall sample sizes for large (>1 kg) burbot were smaller than those for lake trout, northern pike and walleye (see Appendix Table A1), suggesting that size standardized [THg] is important when making interspecific comparisons, and multiple size standards should be used to ensure observed trends hold true at different sizes. My study fish were sampled to span the target 1 kg standard size, which presented a challenge when trying to analyze the data using smaller or larger standard sizes. Although overall sample sizes were lower when analyzing at different standard weights, I was able to demonstrate that using smaller or larger standard sizes did not alter my results greatly, further supporting the interspecific [THg] differences observed among my study species.

Food web effects

Trophic position is commonly used as an indicator of muscle [THg] in fish (Kidd et al. 1995; Eagles-Smith et al. 2008; Rolfhus et al. 2011; Kidd et al. 2012). Individual fish, or species, with higher $\delta^{15}N$ often have higher concentrations of muscle [THg]. Burbot held the highest trophic position and also had the highest concentration of muscle THg. In contrast, northern pike held the lowest trophic position and had the lowest mean muscle [THg]. Lake trout, however, held an identical trophic position to that of burbot, but had [THg] similar to that of northern pike. I found the lack of significant correlation between $\delta^{15}N$ and [THg] in lake trout to be unexpected. Stomach contents of the lake trout sampled in this study were predominantly comprised of fish, ruling out a zooplanktivorous or insectivorous diet to explain the lower levels of [THg] (Cabana et al. 1994). The range of mean population $\delta^{15}N$ for lake trout across all 27 lakes was also low

(see Chapter 1), therefore trophic variation could not explain the lack of correlation (Dufour et al. 2001). The possible lack of diversity in prey consumption (Appendix Table A2) could perhaps explain the absence of a relationship between [THg] and $\delta^{15}N$ in lake trout (Dufour et al. 2001, McIntyre and Beauchamp 2007). Lake trout feed preferentially on cisco (*Coregonus artedi*) and lake whitefish (*C. clupeaformis*), which both have low mercury concentrations (MOECC 2016). While most of the lake trout sampled for my study were large (> 1 kg), and likely preying on larger prey, the prey consumed were not necessarily elevated in mercury. The relationship between mercury and trophic position, and trophic position and body size in lake trout, warrants further research.

Among 1 kg standardized species, the best predictive model of muscle [THg] among all four predator species included both $\delta^{15}N$ and LGR, suggesting that both these variables are important in determining among species variability. This is not surprising given that both predictor variables are strongly correlated with [THg] at an intraspecific level, and may be correlated to one another at the individual species level, as was found to be the case for burbot and walleye. However, the weak evidence ratio between the top-ranked model and the second model suggests that there is little support for the best model, and a model with $\delta^{15}N$ only may be a good alternative. Relative to growth rate, food web position (inferred from $\delta^{15}N$ and $\delta^{13}C$) was also a better predictor of [THg]. This implies that food web position, and overall feeding ecology may be more important than species-specific growth in determining mercury variability among co-occurring piscivorous fish in Boreal systems. However, when models were ranked to compare baseline correction methods using a subset of lakes (n = 7 lakes), in both analyses LGR was the strongest predictor of [THg], indicating that the different result was likely due to

small sample size (n = 7) and not the method used to baseline adjust $\delta^{15}N$ and $\delta^{13}C$. When models were ranked using a slightly larger subset of lakes with 500 g (n = 13 lakes) and 1500 g (n = 21 lakes) size standards, $\delta^{15}N$ was still the leading predictor of variance in muscle [THg] among the four study species. These results support the hypothesis that interspecific differences in muscle mercury concentrations of predatory fish are more strongly related to differences in their trophic ecologies than differences in their growth rates.

Mean population size-adjusted $\delta^{13}C$ values were significantly different across five of the possible six paired species combinations. Burbot and walleye, high [THg] species, had near identical mean $\delta^{13}C$ signatures, but intraspecifically, there was no relationship between [THg] and $\delta^{13}C$ for either high [THg] species. Interspecifically, energy source, inferred by $\delta^{13}C$, was not found to be a good predictor of [THg] on its own. The among-species pattern of mean $\delta^{13}C$ signatures was not surprising, and reflected the habitat and feeding preferences of all four species. As discussed in Chapter 1, carbon signatures follow a horizontal gradient from more negative in offshore (pelagic) zones to more positive in nearshore (littoral) zones. The position of each species within isotopic space mirrored the trophic ecology expected given the individual species foraging and habitat preferences. While the spread of all four species across a carbon gradient does make sense in terms of trophic ecology, these species are all omnivorous and opportunistic feeders to some extent (Scott and Crossman 1973). Chumchal and Hambright (2009) also found no relationship between [THg] and $\delta^{13}C$ in the fish assemblage of a subtropical reservoir; however, they hypothesized that this was because their study lake was shallower and more vegetated compared to other systems in the literature (Power et al.,

2002; Gorski et al., 2003), which resulted in a heightened level of omnivory across their study species. My study lakes vary in area, depth and shape, but are all meso-oligotrophic, and the observed nitrogen ranges across all lakes, and also among the largest and deepest lakes (i.e. Sturgeon, Temagami and Missinaibi), were quite variable (see Chapter 1). This suggests that the level of omnivory alone could not explain the absence of a relationship between [THg] and $\delta^{13}C$. Thus, I would argue that the lack of correlation between [THg] and $\delta^{13}C$ among upper trophic level species is not a result of the lake morphology, but rather fish mobility. All four of my study species, unlike those in Chumchal and Hambright's (2009) study, are highly mobile and have the capacity to overlap in their broader habitat and feeding ranges (Guzzo et al. 2016). While my study species do have fairly different mean $\delta^{13}C$ signatures, suggesting some level of specialization, this specialization does not appear to be related to how much THg they contain.

Growth rate effects

In general, much of the literature supports the hypothesis that biodilution of mercury occurs when individual fish grow at faster rates (tissue anabolism increases faster than mercury accumulation) (Simoneau et al. 2005, Karimi et al. 2007), but there still remains controversy around whether or not growth can be used as a consistent predictor of fish [THg] (Stafford and Haines 2001). For my two study species with relatively high but similar [THg], walleye grew significantly faster than burbot, and for the two study species with relatively low but similar [THg], northern pike grew significantly faster than lake trout. This result supports the ambiguity in using growth rate as a standalone predictor of [THg]. Intraspecifially, northern pike, the fastest growing

species, was the only species for which [THg] and LGR were not significantly correlated. Stafford and Haines (2001) found [THg] in lake trout and smallmouth bass to be relatively unresponsive to varying growth rates. The authors did, however, report a strong relationship between prey [THg] and predator [THg], suggesting that possible observations of biodilution could be confounded if a species, or individual fish, demonstrated specialized feeding preferences for prey with lower [THg]. Northern pike have been known to exhibit specialized feeding behaviour (Beaudoin et al. 1999), but only in lakes in which the species does not co-occur with walleye, lake trout or burbot (Beaudoin et al. 1999). In systems where northern pike were found to co-habit with lake trout and walleye, stomach contents indicated that northern pike fed on a greater diversity of forage fish species compared to walleye and lake trout (Johnston et al. 2003). In my study lakes, northern pike stomach contents contained diverse fish species (see Appendix Table A2), and even amphibians in some lakes (e.g. Anima Nipissing) (see Chapter 1). The diversity of prey type and species suggest northern pike are an opportunistic and generalist feeder, ruling out the potential for preferential feeding on a single prey type. While not found to be significant, northern pike had the strongest relationship between $\delta^{13}C$ and [THg], which could suggest that the energy source upon which they feed may be less contaminated, supporting the importance of food webs in explaining mercury variability. The warm water temperatures in which northern pike reside may also result in higher elimination rates of [THg] (Trudel and Rasmussen 1997). The lack of relationship observed between LGR and [THg] in northern pike, may also simply be due to species-specific physiology.

Interspecifically, growth rate on its own was a relatively poor predictor of differences in muscle [THg] among co-habiting piscivores in boreal lakes. It could be argued that growth efficiency (weight gain per amount of food ingested) may exhibit a stronger relationship with [THg]; however, adequate data were not available to calculate growth efficiencies in this study. Trudel and Rasmussen (2006) also showed that an increase in both growth rate and/or efficiency will result in a decrease in fish tissue mercury concentration.

Other effects to consider

Growth rate and food web structure have proven to be important predictors of intra- and interspecific [THg] at various scales. In my study, however, they could only explain a small portion of the overall [THg] variability (5-8%) that I observed among burbot, lake trout, northern pike and walleye. I believe the remaining species-specific variance could be explained by other physiological factors. A recent review of 25 different studies demonstrated that mercury assimilation efficiencies in fish can range from 10% to 100% for MeHg(I), and 2% to 51% for Hg(II) (Bradley et al. 2017). The mechanisms that either promote or inhibit mercury assimilation are biological (e.g. prey type, consumption rate and activity costs; Trudel and Rasmussen 2006), environmental (e.g. temperature and DOC; Trudel and Rasmussen 1997; Pickhardt et al. 2006), and chemical (e.g. selenium; Belzile et al. 2006). Because of the various factors which can influence mercury assimilation and depuration in fish, it has proven to be a challenge to understand the relationship between ingested and excreted mercury in non-laboratory studies (Bradley et al. 2017). My field study aimed to compare the relative importance of fish growth rate and food web structure in predicting among species [THg] variability,

while accounting for ecosystem (lake) effects. The variance which was not accounted for by lake or species, however, warrants further study. My results emphasize the complexity of understanding mercury uptake in fish, and support the common conclusion that ecological and biological predictors on their own cannot explain the interspecific variability observed in fish communities (Swanson et al. 2006; Donald et al. 2015).

Conclusion

In closing, it is evident that various ecological and physiological factors, such as trophic position, carbon source and growth rate, have varied effects on fish mercury concentrations at intra- and interspecific scales. Based on data collected from 27 Ontario Boreal Shield lakes, I found that interspecifically, trophic position and somatic growth rate combined were the best predictors of mercury variability among co-habiting predators. Alone, growth rate is not a strong predictor of [THg] variation among predators. Despite the utility of $\delta^{15}N$ in explaining mercury variability, relative to energy source and growth rate, $\delta^{15}N$ can only help explain a small portion of the observed interspecific variation in mercury concentrations. While there are many studies which aim to better explain and understand the dynamics of mercury within freshwater ecosystems, and fish in particular, greater efforts are required to link all the processes (physiological, ecological and environmental) influencing mercury in fish.

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APPENDIX A:

SUPPLEMENTARY TABLES FOR CHAPTER 1

Table A1 Summary of sample years, sample sizes (n), means and ranges for burbot (BUR), lake trout (LT), northern pike (NP) and walleye (WALL) weights (g), ages (years), stable isotope signatures ($\delta^{15}N$ and $\delta^{13}C$, ‰) and carbon and nitrogen ratios (C:N, ‰) for all 27 sample lakes. Sample sizes for $\delta^{13}C$ and C:N are the same as those for $\delta^{15}N$, and therefore only presented once.

Lake/Species	Year Sampled	Weight			Age			$\delta^{15}N$			$\delta^{13}C$		C:N	
		n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Range	Mean	Range
Anima Nipissing														
BUR	2009, 2016	28	334	68 - 1460	17	8	2 - 15	18	9.0	6.6 - 10.3	-24	-27.6 - -22.3	3	3.2 - 3.3
LT	2009, 2016	35	1740	22 - 9600	35	10	1 - 23	15	9.6	8.9 - 10.5	-27	-28.7 - -25.0	4	3.2 - 4.8
NP	2009, 2016	18	2776	590 - 8500	16	5	2 - 11	14	8.7	8.1 - 9.2	-25	-28.7 - -22.8	3	3.2 - 3.4
WALL	2009, 2014	315	334	21 - 3800	125	4	1 - 20	13	9.0	7.0 - 13.1	-25	-29.1 - -22.1	3	3.2 - 3.6
Bending														
BUR	2009, 2010	41	811	300 - 2790	41	10	5 - 19	10	9.8	9.1 - 10.9	-27	-28.3 - -26.4	3	3.2 - 3.4
LT	2009, 2010	16	1956	557 - 3350	15	16	8 - 34	11	10.7	9.4 - 12.0	-27	-28.7 - -26.1	3	3.2 - 3.9
NP	2009, 2010	22	1744	125 - 4463	18	7	2 - 14	12	9.3	8.4 - 10.1	-26	-26.7 - -24.6	3	3.1 - 3.3
WALL	2009, 2010	172	396	27 - 2800	76	6	2 - 14	11	8.7	7.2 - 10.5	-27	-28.5 - -25.2	3	3.1 - 3.4
Bigwood														
BUR	2010, 2015	26	856	270 - 3329	22	8	4 - 14	17	10.7	9.2 - 12.1	-26	-27.2 - -24.4	3	3.1 - 3.4
LT	2010, 2015	27	440	55 - 875	27	6	3 - 11	14	9.8	8.8 - 10.7	-28	-32.5 - -26.8	3	3.2 - 3.7
NP	2010, 2015	21	548	103 - 1148	19	2	1 - 6	15	8.7	7.8 - 9.5	-26	-28.4 - -25.0	3	3.1 - 3.4
WALL	2010, 2015	32	839	210 - 3194	32	5	1 - 14	17	9.8	8.2 - 11.3	-26	-27.5 - -24.6	3	3.2 - 3.4
CasselsRabbit														
BUR	2009, 2016	49	424	64 - 1250	30	5	3 - 14	24	10.6	8.4 - 12.4	-28	-28.8 - -24.7	3	3.1 - 3.4
LT	2009, 2016	83	715	25 - 3975	82	7	2 - 27	22	11.3	10.2 - 13.0	-29	-29.7 - -28.2	3	3.0 - 4.0
NP	2009, 2016	51	1218	71 - 3250	45	4	1 - 7	23	9.6	8.0 - 12.8	-27	-28.2 - -25.9	3	3.1 - 3.4
WALL	2009, 2016	234	465	17 – 4050	184	4	1 – 15	24	9.3	8.0 - 11.3	-28	-29.1 - -26.1	3	3.1 - 3.5
Endikai														

Lake/Species	Year Sampled	Weight			Age			$\delta^{15}N$			$\delta^{13}C$		C:N	
		n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Range	Mean	Range
BUR	2008, 2011	69	356	70 - 705	59	13	2 - 22	10	12.0	10.2 - 13.6	-25	-26.6 - -21.7	3	3.3 - 3.5
LT	2008, 2010	35	442	18 - 1620	34	9	4 - 16	13	10.9	10.5 - 11.5	-27	-27.0 - -26.1	3	3.2 - 3.6
NP	2008, 2010	18	2385	28 - 6300	18	5	1 - 8	10	9.7	8.5 - 11.2	-25	-27.1 - -23.1	3	3.2 - 3.3
WALL	2008, 2010	55	488	47 - 4400	53	3	1 - 14	13	9.5	8.0 - 10.7	-25	-26.0 - -23.1	3	3.1 - 3.3
Goldie														
BUR	2011, 2014	11	466	36 - 920	11	7	1 - 11	11	9.8	7.2 - 10.5	-27	-27.4 - -25.8	3	3.2 - 3.3
LT	2011, 2012	16	2349	46 - 4600	16	13	2 - 29	12	11.0	9.7 - 11.7	-28	-29.4 - -26.3	3	3.2 - 4.6
NP	2011, 2012	45	1730	110 - 7600	16	7	3 - 10	10	9.7	8.1 - 10.5	-27	-28.0 - -25.0	3	3.0 - 3.2
WALL	2011, 2012	33	725	42 - 2600	16	4	1 - 7	13	9.7	7.4 - 10.7	-27	-28.6 - -25.9	3	3.1 - 3.5
Kagianagami														
BUR	2011, 2011	20	660	70 - 1100	20	7	3 - 10	10	9.9	8.6 - 10.5	-27	-28.2 - -25.3	3	3.2 - 3.2
LT	2011, 2016	13	2578	359 - 5500	13	15	6 - 31	13	11.6	11.0 - 12.4	-28	-30.0 - -26.5	4	3.2 - 4.3
NP	2011, 2011	20	1972	1100 - 4050	14	6	3 -10	10	9.7	8.0 - 10.9	-25	-26.7 - -22.6	3	3.2 - 3.2
WALL	2011, 2011	20	757	62 - 2550	20	6	1 - 22	10	9.6	8.6 - 11.3	-27	-28.4 - -25.1	3	3.1 - 3.2
Kwinkwaga														
BUR	2011, 2017	40	1166	450 - 2200	23	7	3 - 12	16	11.1	10.0 - 11.7	-29	-30.0 - -28.5	3	3.1 - 3.3
LT	2011, 2017	15	2926	340 - 6400	15	14	5 - 31	12	11.7	11.0 - 12.3	-30	-32.2 - -29.5	4	3.2 - 4.5
NP	2011, 2016	37	1620	460 - 4000	37	6	2 - 11	10	10.0	9.1 - 10.9	-29	-30.5 - -27.8	3	3.0 - 3.1
WALL	2011, 2017	298	405	36 - 3550	129	5	1 - 13	10	10.4	9.7 - 11.3	-29	-30.1 - -27.5	3	3.0 - 3.2
Mameigwess														
BUR	2009, 2016	66	966	150 - 2044	63	11	4 - 23	12	9.3	8.1 - 9.9	-24	-25.1 - -21.1	3	3.2 - 3.3
LT	2009, 2016	150	1713	98 - 14706	113	14	3 - 35	12	9.7	8.5 - 10.9	-25	-26.1 - -23.1	4	3.3 - 5.0
NP	2009, 2016	54	2469	69 - 9805	35	5	2 - 12	10	7.8	7.1 - 8.9	-21	-21.9 - -19.3	3	3.2 - 3.2
WALL	2009, 2016	120	1902	167 - 4500	101	8	2 - 22	12	8.4	6.1 - 8.9	-25	-28.1 - -21.6	4	3.2 - 5.0

Lake/Species	Year Sampled	Weight			Age			$\delta^{15}N$			$\delta^{13}C$		C:N	
		n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Range	Mean	Range
McInnes														
BUR	2011, 2016	21	649	190 - 1980	21	11	3 - 19	19	8.8	7.4 - 9.9	-26	-27.2 - -23.3	3	3.1 - 3.3
LT	2011, 2016	19	4054	1575 - 8600	19	28	21 - 37	19	11.2	10.4 - 12.1	-26	-28.9 - -25.0	3	3.1 - 4.0
NP	2011, 2011	10	892	370 - 1580	10	5	3 - 6	10	8.8	7.8 - 9.4	-25	-27.4 - -23.0	3	3.1 - 3.2
WALL	2011, 2011	21	449	33 - 1500	21	7	1 - 16	10	8.5	7.3 - 9.3	-27	-28.3 - -25.2	3	3.1 - 3.2
McKay														
BUR	2010, 2012	55	1270	203 - 3200	55	10	3 - 19	10	11.4	10.2 - 12.1	-29	-29.2 - -28.4	3	3.2 - 3.3
LT	2010, 2012	14	3580	2200 - 5500	14	15	7 - 22	11	11.9	11.4 - 12.8	-29	-31.8 - -27.8	4	3.2 - 5.0
NP	2010, 2012	53	1471	87 - 6300	42	4	1 - 12	10	9.7	8.7 - 10.2	-29	-29.4 - -27.9	3	3.1 - 3.5
WALL	2010, 2012	299	678	27 - 3948	230	6	2 - 24	10	10.5	9.5 - 12.1	-28	-29.1 - -26.6	3	3.0 - 3.2
Missinaibi														
BUR	2009, 2016	101	887	66 - 2266	25	11	4 - 22	17	11.9	10.9 - 12.7	-27	-27.5 - -25.5	3	3.1 - 3.4
LT	2009, 2016	38	2754	190 - 7000	38	14	5 - 33	15	12.1	11.5 - 12.8	-26	-29.0 - -23.9	4	3.3 - 4.6
NP	2009, 2016	89	1487	280 - 3600	84	6	2 - 11	15	10.1	8.2 - 11.5	-25	-27.1 - -24.0	3	3.1 - 3.4
WALL	2009, 2016	336	663	29 - 3300	131	8	1 - 27	13	10.8	8.9 - 12.8	-26	-27.9 - -21.8	3	3.2 - 3.5
O'sullivan														
BUR	2009, 2016	16	978	170 - 2050	15	8	4 - 16	11	10.9	9.9 - 11.7	-29	-30.2 - -28.1	3	3.2 - 3.3
LT	2009, 2016	14	2810	920 - 4500	13	19	13 - 29	13	12.4	11.2 - 13.6	-30	-31.8 - -29.1	4	3.1 - 4.8
NP	2009, 2009	15	1583	620 - 3300	15	5	2 - 9	10	11.2	10.4 - 12.3	-29	-30.2 - -28.1	3	3.2 - 3.3
WALL	2009, 2009	16	1329	60 - 2650	15	9	2 - 15	10	10.7	9.6 - 12.0	-30	-30.4 - -29.2	3	3.2 - 3.5
Pagwachuan														
BUR	2012, 2016	70	845	172 - 2250	19	9	5 - 19	17	10.5	9.0 - 11.5	-28	-28.9 - -27.3	3	3.1 - 3.3
LT	2012, 2012	12	2754	1500 - 4400	12	16	6 - 32	12	11.7	6.2 - 13.1	-30	-31.7 - -25.0	5	3.3 - 5.4
NP	2012, 2016	17	1651	105 - 3800	17	4	1 - 8	15	9.0	7.5 - 11.9	-28	-33.0 - -25.4	3	3.2 - 4.1

Lake/Species	Year Sampled	Weight			Age			$\delta^{15}N$			$\delta^{13}C$		C:N	
		n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Range	Mean	Range
WALL	2012, 2012	147	506	35 - 3150	49	5	1 - 22	10	9.8	8.1 - 11.4	-27	-28.0 - -24.2	3	3.1 - 3.3
Panache														
BUR	2007, 2014	193	691	166 - 2530	117	8	3 - 17	15	11.0	8.2 - 12.6	-25	-25.7 - -23.3	3	3.1 - 3.3
LT	2010, 2014	65	885	42 - 6500	64	8	3 - 27	10	11.3	10.9 - 12.2	-26	-27.3 - -25.5	3	3.1 - 3.5
NP	2010, 2014	40	1694	246 - 5150	39	5	1 - 13	13	10.3	9.8 - 11.8	-25	-26.6 - -24.4	3	3.1 - 3.4
WALL	2010, 2014	59	1484	33 - 3500	57	6	1 - 19	16	10.2	8.6 - 11.6	-26	-27.7 - -23.8	3	3.0 - 3.6
Radisson														
BUR	2009, 2016	119	474	70 - 1081	14	14	6 - 19	20	10.5	9.9 - 11.1	-26	-26.4 - -25.4	3	3.0 - 3.2
LT	2009, 2014	62	844	46 - 2400	61	11	4 - 31	10	10.7	10.0 - 11.6	-26	-27.4 - -24.1	3	3.1 - 3.5
NP	2009, 2014	18	1543	127 - 7100	16	5	1 - 11	10	9.3	8.0 - 11.0	-24	-26.4 - -21.8	3	3.1 - 3.1
WALL	2009, 2014	36	1116	77 - 3720	33	4	1 - 11	10	9.0	8.5 - 9.8	-25	-26.3 - -22.5	3	2.9 - 3.2
Raven														
BUR	2009, 2015	80	1442	480 - 3011	20	10	6 - 17	10	12.6	11.9 - 13.1	-27	-27.8 - -26.1	3	3.1 - 3.5
LT	2009, 2015	30	1006	50 - 2650	26	12	3 - 25	13	12.0	9.3 - 13.0	-28	-28.4 - -27.2	3	3.2 - 3.6
NP	2009, 2015	19	1126	220 - 5800	17	3	1 - 11	10	10.0	8.9 - 11.5	-26	-27.0 - -24.5	3	3.1 - 3.2
WALL	2009, 2015	90	857	50 - 4025	87	5	1 - 17	10	11.0	9.8 - 12.1	-27	-28.0 - -27.0	3	3.2 - 3.4
Rib														
BUR	2009, 2016	58	438	150 - 1451	19	9	4 - 18	16	9.5	7.9 - 10.3	-26	-26.7 - -24.6	3	3.2 - 3.5
LT	2009, 2016	38	786	30 - 2450	37	8	2 - 14	12	9.6	8.7 - 10.8	-27	-27.9 - -26.5	4	3.3 - 3.9
NP	2009, 2016	24	1153	85 - 6100	24	4	1 - 13	13	8.9	7.3 - 10.0	-26	-28.2 - -23.1	3	3.2 - 3.4
WALL	2009, 2014	140	486	33 - 5200	116	3	1 - 19	10	7.9	7.2 - 10.8	-26	-26.6 - -24.8	3	3.0 - 3.3
Rollo														
BUR	2009, 2017	80	579	63 - 1670	30	10	3 - 18	10	10.8	9.7 - 11.4	-27	-27.4 - -25.2	3	3.1 - 3.3
LT	2009, 2017	23	1183	41 - 3953	23	10	3 - 19	12	11.5	10.8 - 12.7	-27	-28.8 - -26.7	3	3.2 - 4.1

Lake/Species	Year Sampled	Weight			Age			$\delta^{15}N$			$\delta^{13}C$		C:N	
		n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Range	Mean	Range
NP	2009, 2014	20	1510	617 - 4200	20	6	3 -10	11	9.4	8.9 - 9.7	-26	-27.6 - -24.1	3	3.1 - 3.2
WALL	2009, 2014	63	752	36 - 2075	49	4	1 -12	10	9.8	9.0 - 11.0	-26	-27.3 - -24.5	3	3.1 - 3.3
Scotia														
BUR	2010, 2011	23	659	400 - 1285	20	11	5 - 15	10	11.3	10.7 - 11.9	-26	-26.2 - -25.2	3	3.1 - 3.3
LT	2010, 2011	16	1416	290 - 4000	13	11	4 - 38	16	11.5	10.9 - 12.3	-27	-28.5 - -25.4	3	3.2 - 3.9
NP	2010, 2011	19	1388	142 - 3922	18	5	1 - 9	14	9.7	8.3 - 11.2	-26	-28.3 - -24.4	3	3.1 - 3.3
WALL	2010, 2011	18	1111	310 - 2882	18	4	2 -10	13	9.6	8.5 - 10.8	-26	-27.0 - -25.6	3	3.2 - 3.3
Stull														
BUR	2009, 2012	35	726	150 - 2431	33	9	4 - 17	19	11.1	10.1 - 11.8	-28	-28.6 - -27.0	3	3.1 - 3.3
LT	2009, 2012	22	1122	118 - 3100	21	10	5 - 21	17	11.0	10.1 - 11.5	-29	-31.1 - -28.3	4	3.2 - 5.3
NP	2009, 2012	19	1053	106 - 3788	14	2	0 - 7	10	9.3	8.2 - 10.3	-29	-29.1 - -27.8	3	3.1 - 3.2
WALL	2009, 2012	19	890	74 - 2650	19	2	0 - 7	17	8.4	6.9 - 10.5	-28	-28.7 - -25.4	3	3.2 - 3.5
Sturgeon														
BUR	2009, 2016	436	628	35 - 2588	416	9	3 - 21	16	9.7	8.7 - 10.5	-26	-27.0 - -25.0	3	3.2 - 3.3
LT	2009, 2016	92	2599	255 - 8837	76	17	4 - 41	14	10.6	9.9 - 11.3	-27	-28.5 - -26.2	4	3.2 - 4.2
NP	2009, 2016	94	1485	82 - 5131	87	5	2 - 13	14	8.9	8.5 - 9.7	-24	-25.5 - -22.8	3	3.1 - 3.3
WALL	2009, 2016	587	875	33 - 3465	491	6	1 - 21	17	9.4	8.1 - 10.2	-26	-26.9 - -23.8	3	3.2 - 3.4
Temagami														
BUR	2009, 2017	43	367	114 - 959	26	8	4 - 14	14	9.5	7.8 - 10.3	-24	-25.7 - -21.5	3	3.2 - 3.5
LT	2009, 2016	114	1131	24 - 11200	111	10	2 - 27	23	10.4	9.5 - 12.2	-26	-28.2 - -25.2	4	3.0 - 4.6
NP	2009, 2016	24	2011	317 - 4500	24	5	2 - 9	19	9.0	7.5 - 10.2	-24	-26.5 - -21.3	3	2.9 - 3.5
WALL	2009, 2016	193	553	20 - 5600	142	4	1 - 58	20	8.8	7.5 - 11.4	-25	-26.4 - -22.0	3	3.0 - 3.5
Titmarsh														
BUR	2008, 2016	33	573	75 - 1571	30	8	3 - 14	11	9.7	7.3 - 10.8	-24	-25.4 - -23.2	3	3.2 - 3.4

Lake/Species	Year Sampled	Weight			Age			$\delta^{15}N$			$\delta^{13}C$		C:N	
		n	Mean	Range	n	Mean	Range	n	Mean	Range	Mean	Range	Mean	Range
LT	2008, 2016	82	1483	14 - 7000	70	13	4 - 37	11	10.1	9.2 - 11.3	-24	-25.3 - -22.2	3	3.2 - 4.1
NP	2008, 2017	21	1920	480 - 7500	21	4	2 - 13	10	7.9	6.6 - 8.9	-23	-24.1 - -21.3	3	3.2 - 3.2
WALL	2008, 2016	176	1174	41 - 4000	159	6	1 - 20	13	8.0	6.9 - 9.7	-24	-25.5 - -22.8	3	3.2 - 3.3
Trout														
BUR	2009, 2016	128	649	120 - 1680	118	10	4 - 17	20	8.7	8.0 - 9.2	-25	-25.8 - -23.7	3	3.1 - 3.2
LT	2009, 2016	129	2680	470 - 7517	101	20	4 - 36	19	10.5	9.4 - 11.4	-25	-27.3 - -23.0	4	3.0 - 4.4
NP	2009, 2016	100	1830	139 - 6616	94	6	1 - 14	13	8.3	7.5 - 9.4	-22	-24.4 - -19.3	3	3.1 - 3.2
WALL	2009, 2016	611	862	33 - 3000	526	9	1 - 23	20	8.9	8.3 - 9.5	-25	-25.6 - -22.7	3	3.1 - 3.3
Wanapitei														
BUR	2007, 2016	224	1136	97 - 2484	128	12	4 - 27	60	12.9	10.5 - 14.0	-25	-25.7 - -22.3	3	3.2 - 3.4
LT	2009, 2016	32	1003	36 - 3000	30	11	3 - 37	10	12.3	11.4 - 12.9	-27	-27.6 - -25.6	4	3.2 - 4.3
NP	2009, 2011	18	1378	813 - 2638	18	4	2 - 7	11	10.1	9.3 - 10.4	-26	-27.3 - -23.2	3	3.2 - 3.3
WALL	2009, 2016	76	919	27 - 3072	69	5	1 - 27	12	11.2	9.2 - 13.0	-25	-26.3 - -21.6	3	3.2 - 3.7
Winnange														
BUR	2010, 2016	40	485	130 - 1220	36	10	5 - 18	12	9.3	7.8 - 10.1	-24	-24.9 - -21.2	3	3.1 - 3.2
LT	2010, 2016	60	1600	249 - 6162	43	15	5 - 36	12	10.1	9.0 - 11.6	-25	-25.9 - -23.1	4	3.3 - 4.6
NP	2010, 2015	72	1686	71 - 6843	57	6	2 - 14	10	8.0	7.4 - 9.2	-23	-25.1 - -20.9	3	3.0 - 3.3
WALL	2010, 2015	36	1240	33 - 4786	23	5	2 - 18	10	7.9	7.5 - 8.6	-25	-25.1 - -24.4	3	3.0 - 3.4

Table A2 Individual fish stomach contents and body size (total length, TL, and weight, RWT) recorded for burbot (BUR), lake trout (lake trout), northern pike (NP) and walleye (WALL) for 25 of the 28 study lakes. Primary prey represents the largest proportion of stomach content volume, and secondary prey the remaining identifiable stomach content. UIF = unidentifiable fish, UIB = unidentifiable benthic invertebrate.

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
BUR	Anima Nipissing	2016	14-May	468	945	Burbot	
BUR	Anima Nipissing	2016	14-May	523	1080	Burbot	
BUR	Anima Nipissing	2016	14-May	354	265	Crayfish	
BUR	Anima Nipissing	2016	02-Aug	377	325	Sculpin	
BUR	Anima Nipissing	2016	14-May	291	152	UIB	
BUR	Anima Nipissing	2016	02-Aug	223	68	UIF	
BUR	Anima Nipissing	2016	02-Aug	388	305	UIF	
BUR	Bending	2009	18-Oct	393	460	Sculpin	
BUR	Bending	2009	18-Oct	465	820	UIF	
BUR	Bending	2009	18-Oct	418	500	UIF	
BUR	Bending	2009	18-Oct	414	480	Zooplankton	
BUR	Bending	2009	18-Oct	365	400	Zooplankton	
BUR	Bending	2009	18-Oct	409	500	Zooplankton	
BUR	Bigwood	2012	30-May	594	1365	Crayfish	
BUR	Bigwood	2012	30-May	606	1483	Crayfish	
BUR	Bigwood	2011	25-Sep	617	1787.5	UIF	
BUR	Endikai	2010	21-Apr	380	300	UIB	
BUR	Endikai	2010	21-Apr	339	220	UIB	
BUR	Endikai	2010	21-Apr	377	320	UIB	
BUR	Goldie	2014	01-Oct	479	920	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
BUR	Kagianagami	2011	07-Sep	533	1060	Cisco	
BUR	Kagianagami	2011	07-Sep	470	780	Cisco	Slimy sculpin
BUR	Kagianagami	2011	07-Sep	395	420	Cisco	
BUR	Kagianagami	2011	07-Sep	467	800	Cisco	
BUR	Kagianagami	2011	07-Sep	543	1100	Crayfish	
BUR	Kagianagami	2011	07-Sep	230	70	Midges	Caddisflies
BUR	Kagianagami	2011	07-Sep	502	920	Ninespine stickleback	
BUR	Kagianagami	2011	07-Sep	370	340	Slimy sculpin	Ninespine stickleback
BUR	Kagianagami	2011	07-Sep	445	640	UIF	
BUR	Kagianagami	2011	07-Sep	490	800	UIF	
BUR	Kagianagami	2011	07-Sep	431	650	UIF	
BUR	Mameigwess	2016	22-Jun	670	1750	Crayfish	
BUR	Mameigwess	2016	22-Jun	593	1350	Sculpin	
BUR	Mameigwess	2016	22-Jun	662	1950	UIF	
BUR	Mameigwess	2016	22-Jun	474	600	UIF	
BUR	McInnes	2011	11-Aug	556	1060	Cisco	
BUR	McInnes	2011	11-Aug	458	550	Cisco	
BUR	McInnes	2016	09-Sep	615	1360	Crayfish	UIF
BUR	McInnes	2016	09-Sep	353	280	UIB	
BUR	McInnes	2016	09-Sep	377	325	UIB	
BUR	McInnes	2016	09-Sep	481	630	UIB	UIF
BUR	McInnes	2016	09-Sep	314	205	UIB	
BUR	McInnes	2011	11-Aug	444	375	UIB	UIF
BUR	McInnes	2016	09-Sep	388	330	UIF	
BUR	McInnes	2011	11-Aug	518	830	UIF	
BUR	McKay	2010	28-May	577	1320	Cisco	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
BUR	McKay	2010	28-May	555	1140	Cisco	
BUR	McKay	2010	28-May	661	1520	Crayfish	
BUR	McKay	2010	28-May	684	2250	UIF	
BUR	O'Sullivan	2009	14-Oct	546	1100	Cisco	Stickleback
BUR	O'Sullivan	2016	09-Jun	645	1940	Sculpin	
BUR	Pagwachuan	2016	10-Jun	606	980	Crayfish	
BUR	Pagwachuan	2016	10-Jun	415	440	Sculpin	
BUR	Pagwachuan	2016	10-Jun	498	670	UIF	
BUR	Pagwachuan	2016	10-Jun	454	580	UIF	
BUR	Pagwachuan	2016	10-Jun	521	750	UIF	
BUR	Pagwachuan	2016	10-Jun	474	660	UIF	
BUR	Pagwachuan	2016	10-Jun	401	380	UIF	
BUR	Pagwachuan	2016	10-Jun	437	550	UIF	
BUR	Rabbit	2016	24-May	416	480	Crayfish	UIB
BUR	Rabbit	2016	24-May	594	1250	Crayfish	Sculpin
BUR	Rabbit	2016	24-May	390	370	Crayfish	UIB
BUR	Rabbit	2016	24-May	465	570	Crayfish	
BUR	Rabbit	2016	24-May	449	520	Crayfish	
BUR	Rabbit	2016	24-May	350	250	Crayfish	
BUR	Rabbit	2016	24-May	380	340	Crayfish	
BUR	Rabbit	2016	24-May	423	560	Crayfish	
BUR	Rabbit	2016	24-May	375	270	Crayfish	
BUR	Rabbit	2016	24-May	276	124	Crayfish	
BUR	Rabbit	2016	24-May	410	440	Crayfish	UIB
BUR	Rabbit	2016	24-May	415	460	Crayfish	Sculpin
BUR	Rabbit	2016	24-May	527	880	Sculpin	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
BUR	Rabbit	2016	24-May	273	164	Sculpin	
BUR	Radisson	2016	08-Aug	503	750	Sculpin	UIF
BUR	Radisson	2016	08-Aug	465	550	UIB	UIF
BUR	Radisson	2016	08-Aug	441	560	UIF	
BUR	Radisson	2016	08-Aug	485	585	UIF	
BUR	Radisson	2016	08-Aug	471	580	UIF	
BUR	Radisson	2016	08-Aug	489	660	UIF	
BUR	Radisson	2016	08-Aug	475	590	UIF	
BUR	Radisson	2016	08-Aug	356	290	UIF	
BUR	Radisson	2016	08-Aug	546	900	UIF	
BUR	Radisson	2016	08-Aug	463	510	UIF	
BUR	Raven	2009	20-Jul	599	1360	UIF	
BUR	Raven	2009	20-Jul	636	1900	UIF	
BUR	Raven	2009	20-Jul	570	1420	UIF	
BUR	Rib	2016	09-May	459	475	Caddisflies	
BUR	Rib	2016	09-May	415	420	Crayfish	
BUR	Rib	2016	09-May	200	190	Crayfish	
BUR	Rib	2016	09-May	321	175	Crayfish	
BUR	Rib	2016	09-May	415	395	Crayfish	Dragonflies and mayflies
BUR	Rib	2016	09-May	344	239	UIB	
BUR	Rib	2016	09-May	355	250	UIF	
BUR	Rib	2016	09-May	307	154	UIF	
BUR	Rib	2016	09-May	314	158	UIF	
BUR	Rib	2016	09-May	374	320	UIF	
BUR	Rollo	2017	13-Mar	615	1670	Crayfish	
BUR	Rollo	2017	13-Mar	552	1198	Crayfish	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
BUR	Rollo	2017	13-Mar	490	777	Crayfish	
BUR	Rollo	2017	13-Mar	459	628	Crayfish	
BUR	Rollo	2017	13-Mar	520	850	Crayfish	UIF
BUR	Rollo	2017	13-Mar	443	645	Crayfish	
BUR	Rollo	2017	13-Mar	521	1159	UIB	
BUR	Scotia	2011	29-Jun	472	680.7	Crayfish	
BUR	Scotia	2011	29-Jun	499	788.8	UIF	UIF
BUR	Sturgeon	2016	02-Jul	290	358	Sculpin	
BUR	Sturgeon	2016	02-Jul	445	600	UIB	
BUR	Sturgeon	2016	02-Jul	532	1040	UIB	
BUR	Sturgeon	2016	02-Jul	419	510	UIB	
BUR	Sturgeon	2016	06-Jul	534	930	UIB	
BUR	Sturgeon	2016	02-Jul	571	1050	UIF	
BUR	Sturgeon	2016	02-Jul	418	520	UIF	
BUR	Sturgeon	2016	02-Jul	612	1460	UIF	
BUR	Sturgeon	2016	06-Jul	354	325	UIF	
BUR	Temagami	2016	31-May	475	650	Crayfish	
BUR	Temagami	2017	20-Mar	493	780	Crayfish	
BUR	Temagami	2016	31-May	377	300	UIB	
BUR	Temagami	2016	31-May	281	124	UIB	
BUR	Temagami	2016	31-May	423	620	UIF	
BUR	Temagami	2016	31-May	350	260	UIF	UIB
BUR	Temagami	2016	31-May	503	840	UIF	Crayfish
BUR	Temagami	2016	31-May	297	170	UIF	UIB
BUR	Titmarsh	2016	14-Jul	530	1050	Sculpin	
BUR	Titmarsh	2016	14-Jul	430	515	Sculpin	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
BUR	Titmarsh	2016	14-Jul	522	900	Sculpin	
BUR	Titmarsh	2016	14-Jul	362	380	Sculpin	UIF
BUR	Titmarsh	2016	14-Jul	357	300	Sculpin	
BUR	Titmarsh	2016	14-Jul	373	355	Sculpin	
BUR	Titmarsh	2016	14-Jul	314	210	UIB	
BUR	Titmarsh	2016	14-Jul	251	75	UIB	
BUR	Titmarsh	2016	14-Jul	504	820	UIB	
BUR	Titmarsh	2016	14-Jul	477	649	UIF	
BUR	Titmarsh	2016	14-Jul	462	660	UIF	
BUR	Titmarsh	2016	14-Jul	371	370	UIF	
BUR	Titmarsh	2016	14-Jul	371	400	UIF	
BUR	Trout	2016	17-Sep	543	1290	Cisco	Stickleback
BUR	Trout	2016	17-Sep	440	600	Ninespine stickleback	
BUR	Trout	2016	17-Sep	447	640	Sculpin	
BUR	Trout	2016	17-Sep	489	700	Stickleback	
BUR	Trout	2016	17-Sep	516	820	Stickleback	
BUR	Trout	2016	17-Sep	309	200	UIB	
BUR	Trout	2016	17-Sep	405	440	UIB	UIF
BUR	Trout	2016	17-Sep	369	380	UIF	
BUR	Trout	2016	17-Sep	456	685	UIF	
BUR	Trout	2016	17-Sep	462	770	UIF	
BUR	Trout	2016	17-Sep	614	1680	UIF	
BUR	Trout	2016	17-Sep	456	660	UIF	
BUR	Trout	2016	17-Sep	558	1160	UIF	
BUR	Trout	2016	17-Sep	395	470	UIF	
BUR	Wanapitei	2009	28-May	621	1547.6	Crayfish	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
BUR	Wanapitei	2009	28-May	661	1939.5	Crayfish	
BUR	Wanapitei	2009	28-May	715	2125.1	Crayfish	
BUR	Wanapitei	2009	28-May	507	870.2	UIB	Crayfish
BUR	Wanapitei	2009	28-May	620	1633.1	UIF	
BUR	Wanapitei	2009	28-May	571	1215	UIF	
BUR	Winnange	2016	20-Jul	421	470	Sculpin	
BUR	Winnange	2016	20-Jul	454	630	Sculpin	
BUR	Winnange	2016	20-Jul	449	570	UIB	
LT	Anima Nipissing	2016	02-Aug	480	930	Lake whitefish	Burbot and yellow perch
LT	Anima Nipissing	2016	02-Aug	550	1350	Sculpin	
LT	Anima Nipissing	2016	02-Aug	387	365	UIF	
LT	Bending	2009	18-Oct	656	2200	Perch	Walleye
LT	Bending	2009	18-Oct	750	3350	Stickleback	
LT	Bending	2009	18-Oct	581	1540	UIF	
LT	Bending	2009	18-Oct	705	2800	Walleye	Walleye
LT	Bigwood	2011	25-Sep	403	511.7	Phantom midges	
LT	Bigwood	2011	25-Sep	353	376	Phantom midges	
LT	Bigwood	2011	25-Sep	446	724.4	UIB	
LT	Bigwood	2011	25-Sep	376	455.1	UIB	Mayflies and midges
LT	Endikai	2010	21-Apr	600	1620	Smallmouth bass	
LT	Goldie	2012	10-Jul	641	2550	UIF	
LT	Kagianagami	2016	09-Jul	340	359	UIF	Sculpin
LT	Kagianagami	2016	09-Jul	636	2246	UIF	
LT	Kagianagami	2011	07-Sep	631	2350	UIF	
LT	Kagianagami	2011	07-Sep	725	3050	UIF	
LT	Kagianagami	2011	07-Sep	695	2950	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
LT	Mameigwess	2016	22-Jun	495	900	Cisco	
LT	Mameigwess	2016	22-Jun	822	5850	Lake whitefish	
LT	Mameigwess	2016	22-Jun	1050	10500	Lake whitefish	
LT	Mameigwess	2016	22-Jun	313	204	Ninespine stickleback	
LT	Mameigwess	2016	22-Jun	543	1180	Sculpin	Leeches
LT	Mameigwess	2016	22-Jun	252	152	Sculpin	
LT	Mameigwess	2016	22-Jun	246	98	Sculpin	UIF
LT	Mameigwess	2016	22-Jun	522	1190	UIB	
LT	Mameigwess	2016	22-Jun	594	900	UIF	
LT	Mameigwess	2016	22-Jun	387	450	UIF	
LT	Mameigwess	2016	22-Jun	345	280	UIF	
LT	Mameigwess	2016	22-Jun	386	425	UIF	
LT	Mameigwess	2016	22-Jun	601	1810	UIF	
LT	Mameigwess	2016	22-Jun	428	560	UIF	
LT	Mameigwess	2016	22-Jun	297	174	UIF	
LT	McInnes	2011	11-Aug	932	8600	Burbot	
LT	McInnes	2016	09-Sep	890	6300	Cisco	
LT	McInnes	2016	09-Sep	826	4350	UIF	
LT	McInnes	2016	09-Sep	715	2800	UIF	
LT	McInnes	2016	09-Sep	795	4800	UIF	
LT	McInnes	2016	09-Sep	828	4500	UIF	
LT	McInnes	2011	11-Aug	787	4200	UIF	
LT	McInnes	2011	11-Aug	794	4000	UIF	
LT	McInnes	2011	11-Aug	913	5700	UIF	
LT	McInnes	2011	11-Aug	779	4100	UIF	
LT	McKay	2010	28-May	790	5500	Cisco	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
LT	McKay	2010	28-May	645	2450	Cisco	
LT	McKay	2010	28-May	758	3900	UIF	
LT	McKay	2010	28-May	774	3850	UIF	
LT	McKay	2010	28-May	782	4400	UIF	
LT	McKay	2010	28-May	770	4400	UIF	
LT	O'Sullivan	2016	09-Jun	654	2900	Cisco	
LT	O'Sullivan	2009	14-Oct	702	2600	Minnows	
LT	O'Sullivan	2009	14-Oct	668	2250	Stickleback	
LT	O'Sullivan	2016	09-Jun	615	1900	UIF	
LT	O'Sullivan	2009	14-Oct	807	4500	UIF	
LT	O'Sullivan	2009	14-Oct	815	4100	UIF	
LT	Raven	2009	20-Jul	266	125	UIF	
LT	Raven	2009	20-Jul	393	460	UIF	
LT	Rib	2016	09-May	561	1260	Crayfish	
LT	Rib	2016	09-May	531	1100	Mayflies	
LT	Rib	2016	09-May	538	1140	Mayflies	Fish eggs
LT	Rib	2016	09-May	634	1150	Mayflies	
LT	Rib	2016	09-May	513	1000	UIF	UIB
LT	Rib	2016	09-May	663	2450	UIF	
LT	Rib	2016	09-May	522	1020	UIF	Mayflies
LT	Rib	2016	09-May	514	1170	UIF	
LT	Rollo	2017	13-Mar	647	1850	Stickleback	
LT	Rollo	2017	13-Mar	457	800	UIF	
LT	Scotia	2011	29-Jun	591	1914.2	Shiner	
LT	Stull	2012	18-Sep	427	670	Cisco	
LT	Stull	2012	18-Sep	583	1560	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
LT	Stull	2012	18-Sep	556	1540	UIF	
LT	Stull	2012	18-Sep	251	130	UIF	
LT	Stull	2012	09-Jan	382	481.7	UIF	
LT	Sturgeon	2016	06-Jul	360	290	UIB	
LT	Sturgeon	2016	02-Jul	750	2925	UIF	
LT	Sturgeon	2016	02-Jul	640	2225	UIF	
LT	Sturgeon	2016	02-Jul	606	2200	UIF	
LT	Sturgeon	2016	02-Jul	765	4550	UIF	
LT	Sturgeon	2016	02-Jul	790	4600	UIF	
LT	Sturgeon	2016	06-Jul	681	2600	UIF	
LT	Sturgeon	2016	06-Jul	624	1980	UIF	
LT	Sturgeon	2016	06-Jul	625	1940	UIF	
LT	Sturgeon	2016	06-Jul	371	370	UIF	
LT	Temagami	2016	31-May	499	980	Cisco	
LT	Temagami	2016	31-May	721	3350	Cisco	UIF
LT	Temagami	2016	31-May	1025	11200	Lake whitefish	
LT	Temagami	2016	31-May	250	116	Ninespine stickleback	
LT	Temagami	2016	31-May	458	670	Sculpin	UIB
LT	Temagami	2016	31-May	459	720	UIF	
LT	Temagami	2016	31-May	441	620	UIF	
LT	Temagami	2016	31-May	579	1500	UIF	
LT	Temagami	2016	31-May	468	860	UIF	
LT	Temagami	2016	31-May	479	840	UIF	
LT	Titmarsh	2016	14-Jul	673	3050	Sculpin	
LT	Titmarsh	2016	14-Jul	401	475	Sculpin	
LT	Titmarsh	2016	14-Jul	479	840	UIB	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
LT	Titmarsh	2016	14-Jul	556	1220	UIB	
LT	Titmarsh	2016	14-Jul	415	555	UIB	
LT	Titmarsh	2016	14-Jul	414	580	UIB	
LT	Titmarsh	2016	14-Jul	895	7000	UIF	
LT	Titmarsh	2016	14-Jul	447	700	UIF	
LT	Titmarsh	2016	14-Jul	533	1260	UIF	
LT	Titmarsh	2016	14-Jul	549	1260	UIF	
LT	Trout	2016	17-Sep	644	2200	Cisco	
LT	Trout	2016	17-Sep	705	3100	Cisco	
LT	Trout	2016	17-Sep	629	2120	UIB	
LT	Trout	2016	17-Sep	615	2450	UIB	
LT	Trout	2016	17-Sep	711	3300	UIF	
LT	Trout	2016	17-Sep	685	2900	UIF	
LT	Trout	2016	17-Sep	730	2200	UIF	
LT	Trout	2016	17-Sep	606	2300	UIF	
LT	Trout	2016	17-Sep	639	2225	UIF	
LT	Trout	2016	17-Sep	887	7300	UIF	
LT	Winnange	2016	20-Jul	722	3400	UIF	UIB
NP	Anima Nipissing	2016	14-May	864	4500	Lake whitefish	
NP	Anima Nipissing	2016	14-May	1060	8500	Lake whitefish	
NP	Anima Nipissing	2016	14-May	521	740	Perch	
NP	Anima Nipissing	2016	14-May	827	3550	UIF	
NP	Anima Nipissing	2016	14-May	749	2550	UIF	
NP	Anima Nipissing	2016	14-May	598	1200	UIF	
NP	Anima Nipissing	2016	14-May	474	590	UIF	Perch
NP	Anima Nipissing	2016	14-May	550	940	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
NP	Anima Nipissing	2016	14-May	790	3350	UIF	Salamanders
NP	Anima Nipissing	2016	14-May	496	680	UIF	
NP	Anima Nipissing	2016	14-May	624	800	UIF	
NP	Anima Nipissing	2016	14-May	809	3500	Walleye	
NP	Anima Nipissing	2016	14-May	848	3700	White sucker	Salamanders and frogs
NP	Bending	2009	18-Oct	830	2950	Crayfish	
NP	Bending	2009	18-Oct	632	1420	Smallmouth bass	
NP	Bending	2009	18-Oct	598	1060	UIF	
NP	Bending	2009	18-Oct	714	2600	Walleye	
NP	Bigwood	2012	30-May	355	250	UIF	
NP	Endikai	2010	21-Apr	641	2100	Brook trout	
NP	Endikai	2010	21-Apr	565	1180	Burbot	
NP	Endikai	2010	21-Apr	830	3850	Burbot	
NP	Endikai	2010	21-Apr	815	3700	Burbot	
NP	Endikai	2010	21-Apr	885	4650	Burbot	
NP	Endikai	2010	21-Apr	521	800	UIF	
NP	Endikai	2010	21-Apr	556	1060	UIF	
NP	Kagianagami	2011	07-Sep	806	3400	Burbot	
NP	Kagianagami	2011	07-Sep	660	1580	Cisco	
NP	Kagianagami	2011	07-Sep	618	1300	Crayfish	
NP	Kagianagami	2011	07-Sep	878	3750	Lake whitefish	
NP	Kagianagami	2011	07-Sep	684	1480	UIF	
NP	Kagianagami	2011	07-Sep	709	2160	White sucker	
NP	Kagianagami	2011	07-Sep	637	1600	Yellow perch	Burbot
NP	Mameigwess	2016	22-Jun	457	610	UIB	
NP	Mameigwess	2016	22-Jun	798	3600	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
NP	Mameigwess	2016	22-Jun	524	890	UIF	
NP	Mameigwess	2016	22-Jun	848	4600	UIF	
NP	Mameigwess	2016	22-Jun	431	460	UIF	
NP	Mameigwess	2016	22-Jun	683	2500	White sucker	
NP	Mameigwess	2016	22-Jun	517	820	Yellow perch	Frogs and toads
NP	Mameigwess	2016	22-Jun	496	700	Yellow perch	
NP	McInnes	2011	11-Aug	594	1130	Crayfish	
NP	McInnes	2011	11-Aug	605	1040	Crayfish	Yellow perch
NP	McInnes	2011	11-Aug	554	840	Crayfish	
NP	McInnes	2011	11-Aug	529	770	Crayfish	
NP	McKay	2010	28-May	627	1420	Cisco	
NP	McKay	2010	28-May	432	460	Crayfish	
NP	McKay	2010	28-May	774	2120	Crayfish	
NP	McKay	2010	28-May	586	920	UIF	
NP	McKay	2010	28-May	1035	5800	White sucker	
NP	O'Sullivan	2009	14-Oct	631	1460	Cisco	
NP	O'Sullivan	2009	14-Oct	783	2900	UIF	
NP	Pagwachuan	2016	10-Jun	789	2650	Crayfish	Leeches
NP	Pagwachuan	2016	10-Jun	773	2350	Northern pike	
NP	Pagwachuan	2016	10-Jun	679	1750	UIB	Ninespine stickleback
NP	Pagwachuan	2016	10-Jun	634	1580	UIF	UIB
NP	Pagwachuan	2016	10-Jun	426	420	UIF	
NP	Pagwachuan	2016	10-Jun	462	555	UIF	UIB
NP	Pagwachuan	2016	10-Jun	703	1950	UIF	
NP	Panache	2011	21-Jun	642	1702	Cisco	
NP	Panache	2011	21-Jun	629	1493	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
NP	Panache	2011	21-Jun	554	1109	UIF	
NP	Panache	2011	21-Jun	757	2733	UIF	Yellow perch
NP	Panache	2011	21-Jun	761	2691	UIF	
NP	Rabbit	2016	24-May	486	640	Perch	UIB
NP	Rabbit	2016	24-May	782	3250	UIF	
NP	Rabbit	2016	24-May	791	3250	UIF	
NP	Rabbit	2016	24-May	778	3050	UIF	
NP	Rabbit	2016	24-May	666	1860	UIF	
NP	Rabbit	2016	24-May	756	2800	UIF	
NP	Rib	2016	09-May	855	3750	Burbot	
NP	Rib	2016	09-May	672	2050	Burbot	
NP	Rib	2016	09-May	650	1640	Burbot	UIF
NP	Rib	2016	09-May	518	680	UIF	
NP	Rib	2016	09-May	554	995	UIF	
NP	Scotia	2011	29-Jun	555	1026.9	Common shiner	
NP	Scotia	2011	29-Jun	525	738.7	Common shiner	
NP	Sturgeon	2016	06-Jul	601	1210	Crayfish	UIF
NP	Sturgeon	2016	06-Jul	523	880	Crayfish	
NP	Sturgeon	2016	06-Jul	742	1900	Crayfish	
NP	Sturgeon	2016	06-Jul	745	2050	Crayfish	
NP	Sturgeon	2016	02-Jul	466	570	Leeches	
NP	Sturgeon	2016	02-Jul	617	1500	UIF	Leeches
NP	Sturgeon	2016	02-Jul	451	470	UIF	
NP	Sturgeon	2016	02-Jul	628	1380	Yellow perch	UIF
NP	Sturgeon	2016	02-Jul	525	750	Yellow perch	
NP	Temagami	2016	31-May	535	950	Rock bass	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
NP	Temagami	2016	31-May	432	410	UIF	
NP	Temagami	2016	31-May	655	1820	UIF	
NP	Temagami	2016	31-May	831	3700	UIF	Burbot
NP	Temagami	2016	31-May	900	4500	UIF	
NP	Temagami	2016	31-May	526	800	UIF	
NP	Temagami	2016	31-May	742	3250	UIF	
NP	Titmarsh	2016	14-Jul	534	940	Crayfish	UIF
NP	Titmarsh	2016	14-Jul	615	1260	Crayfish	
NP	Titmarsh	2016	14-Jul	496	790	UIB	UIF
NP	Titmarsh	2016	14-Jul	436	480	UIF	
NP	Titmarsh	2017	25-May	682	2100	UIF	
NP	Trout	2016	17-Sep	723	2550	Burbot	
NP	Trout	2016	17-Sep	756	2850	Burbot	
NP	Trout	2016	17-Sep	525	770	Crayfish	
NP	Trout	2016	17-Sep	607	1220	Crayfish	
NP	Trout	2016	17-Sep	565	1100	UIF	Perch
NP	Trout	2016	17-Sep	605	1480	UIF	
NP	Trout	2016	17-Sep	690	2100	Walleye	
NP	Wanapitei	2011	30-May	736	2638	UIF	
NP	Wanapitei	2011	30-May	679	1952	UIF	
NP	Wanapitei	2011	30-May	598	1342	UIF	
WALL	Bending	2009	18-Oct	641	2600	Burbot	
WALL	Bending	2009	18-Oct	388	600	UIF	
WALL	Bending	2009	18-Oct	601	2200	UIF	
WALL	Bending	2009	18-Oct	483	1100	UIF	
WALL	Bending	2009	18-Oct	305	235	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
WALL	Bending	2009	18-Oct	260	145	UIF	
WALL	Bending	2009	18-Oct	458	820	UIF	
WALL	Bending	2009	18-Oct	534	1580	UIF	
WALL	Bending	2009	18-Oct	338	375	UIF	
WALL	Bending	2009	18-Oct	505	1240	UIF	
WALL	Bending	2009	18-Oct	383	480	UIF	
WALL	Bending	2009	18-Oct	675	2800	UIF	
WALL	Bigwood	2011	25-Sep	295	243.4	Caddisflies	
WALL	Bigwood	2011	25-Sep	432	795.2	Dragonflies	
WALL	Bigwood	2012	30-May	400	594	UIF	
WALL	Bigwood	2011	25-Sep	502	1261.7	UIF	
WALL	Bigwood	2011	25-Sep	423	704.5	UIF	
WALL	Endikai	2010	21-Apr	465	860	UIB	
WALL	Endikai	2010	21-Apr	490	1060	UIB	
WALL	Kagianagami	2011	07-Sep	450	850	Cisco	
WALL	Kagianagami	2011	07-Sep	218	84	Darter	
WALL	Kagianagami	2011	07-Sep	434	750	Slimy sculpin	UIF
WALL	Kagianagami	2011	07-Sep	489	1060	UIF	
WALL	Kagianagami	2011	07-Sep	503	1160	UIF	
WALL	Kagianagami	2011	07-Sep	423	690	UIF	
WALL	Kagianagami	2011	07-Sep	419	740	UIF	
WALL	Kagianagami	2011	07-Sep	197	62	UIF	
WALL	Kagianagami	2011	07-Sep	241	116	UIF	
WALL	Kagianagami	2011	07-Sep	358	400	UIF	
WALL	Kagianagami	2011	07-Sep	620	2340	UIF	Crayfish
WALL	Kagianagami	2011	07-Sep	460	820	Yellow perch	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
WALL	Mameigwess	2016	22-Jun	598	1825	UIB	
WALL	Mameigwess	2016	22-Jun	616	2450	UIF	
WALL	Mameigwess	2016	22-Jun	627	2350	UIF	
WALL	Mameigwess	2016	22-Jun	685	3300	UIF	
WALL	Mameigwess	2016	22-Jun	562	1925	UIF	
WALL	Mameigwess	2016	22-Jun	645	2600	UIF	
WALL	McInnes	2011	11-Aug	186	52	Logperch	
WALL	McInnes	2011	11-Aug	245	118	Logperch	
WALL	McInnes	2011	11-Aug	397	515	UIF	
WALL	McInnes	2011	11-Aug	259	130	UIF	
WALL	McInnes	2011	11-Aug	316	245	UIF	
WALL	McInnes	2011	11-Aug	169	33	UIF	
WALL	McInnes	2011	11-Aug	174	42	UIF	
WALL	McInnes	2011	11-Aug	302	222	UIF	
WALL	McInnes	2011	11-Aug	304	222	UIF	
WALL	McInnes	2011	11-Aug	345	375	UIF	
WALL	McKay	2010	28-May	765	3650	Cisco	
WALL	McKay	2010	28-May	519	1160	Darter	
WALL	McKay	2010	28-May	585	1620	Segmented worms	
WALL	McKay	2010	28-May	583	1780	UIF	
WALL	O'Sullivan	2009	14-Oct	629	2050	Cisco	
WALL	O'Sullivan	2009	14-Oct	338	315	UIF	
WALL	O'Sullivan	2009	14-Oct	307	250	UIF	
WALL	Panache	2011	21-Jun	676	3140	Midges	
WALL	Panache	2011	21-Jun	550	1869	Rainbow smelt	
WALL	Panache	2011	21-Jun	685	3496	Rainbow smelt	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
WALL	Panache	2011	21-Jun	514	1490	Rainbow smelt	UIB
WALL	Panache	2011	21-Jun	443	862	UIF	
WALL	Rabbit	2016	24-May	650	2600	UIB	
WALL	Rabbit	2016	24-May	473	940	UIF	
WALL	Scotia	2011	29-Jun	390	576.5	Common shiner	
WALL	Scotia	2011	29-Jun	455	981.2	Shiner	
WALL	Scotia	2011	29-Jun	596	2329.7	Shiner	
WALL	Scotia	2011	29-Jun	408	699.4	UIF	
WALL	Stull	2012	18-Sep	550	2180	Cisco	
WALL	Stull	2012	18-Sep	592	2480	UIF	
WALL	Stull	2012	18-Sep	541	1380	UIF	
WALL	Stull	2012	18-Sep	463	1060	UIF	
WALL	Stull	2012	18-Sep	323	300	UIF	
WALL	Stull	2012	18-Sep	202	74	Yellow perch	
WALL	Sturgeon	2016	02-Jul	577	1480	Ninespine stickleback	
WALL	Sturgeon	2016	02-Jul	594	1600	UIB	
WALL	Sturgeon	2016	02-Jul	576	1540	UIF	Crayfish
WALL	Sturgeon	2016	02-Jul	241	98	UIF	
WALL	Sturgeon	2016	02-Jul	590	1750	UIF	UIB
WALL	Sturgeon	2016	02-Jul	673	2500	UIF	
WALL	Sturgeon	2016	02-Jul	526	1100	UIF	UIB
WALL	Sturgeon	2016	02-Jul	601	1700	UIF	
WALL	Sturgeon	2016	02-Jul	227	87	UIF	
WALL	Sturgeon	2016	02-Jul	408	605	UIF	
WALL	Sturgeon	2016	02-Jul	591	2000	Yellow perch	
WALL	Temagami	2016	31-May	551	840	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
WALL	Temagami	2016	31-May	542	1700	UIF	
WALL	Temagami	2016	31-May	462	900	UIF	
WALL	Temagami	2016	31-May	600	1950	UIF	
WALL	Temagami	2016	31-May	468	1050	UIF	
WALL	Titmarsh	2016	14-Jul	556	1700	Burbot	
WALL	Titmarsh	2016	14-Jul	754	4000	UIF	
WALL	Titmarsh	2016	14-Jul	347	375	UIF	
WALL	Titmarsh	2016	14-Jul	425	715	UIF	
WALL	Titmarsh	2016	14-Jul	521	1375	UIF	
WALL	Titmarsh	2016	14-Jul	628	2300	UIF	
WALL	Titmarsh	2016	14-Jul	417	700	UIF	
WALL	Titmarsh	2016	14-Jul	479	1000	UIF	UIB
WALL	Titmarsh	2016	14-Jul	412	515	UIF	
WALL	Titmarsh	2016	14-Jul	416	610	UIF	
WALL	Titmarsh	2016	14-Jul	394	515	UIF	
WALL	Titmarsh	2016	14-Jul	241	140	Yellow perch	
WALL	Trout	2016	17-Sep	525	1250	Ninespine stickleback	
WALL	Trout	2016	17-Sep	508	1240	Sculpin	
WALL	Trout	2016	17-Sep	530	1480	Sculpin	UIF
WALL	Trout	2016	17-Sep	572	1610	Stickleback	
WALL	Trout	2016	17-Sep	517	1150	UIF	
WALL	Trout	2016	17-Sep	469	790	UIF	
WALL	Trout	2016	17-Sep	486	1080	UIF	UIF
WALL	Trout	2016	17-Sep	577	1750	UIF	
WALL	Trout	2016	17-Sep	546	1380	UIF	
WALL	Trout	2016	17-Sep	503	1120	UIF	

Species	Lake	Year	Date	TL (mm)	RWT (g)	Primary Prey	Secondary Prey
WALL	Trout	2016	17-Sep	474	950	UIF	
WALL	Trout	2016	17-Sep	449	820	UIF	
WALL	Trout	2016	17-Sep	452	795	UIF	
WALL	Trout	2016	17-Sep	536	1140	UIF	
WALL	Trout	2016	17-Sep	536	1310	UIF	
WALL	Trout	2016	17-Sep	555	1500	UIF	
WALL	Trout	2016	17-Sep	585	1600	UIF	
WALL	Trout	2016	17-Sep	558	1500	UIF	
WALL	Trout	2016	17-Sep	511	1040	UIF	
WALL	Wanapitei	2009	28-May	616	2600	Cisco	
WALL	Wanapitei	2009	28-May	618	2200	UIB	Minnows
WALL	Wanapitei	2009	28-May	692	2950	UIF	

Table A3 Summary of all models ranked by second order Akaike Information Criterion (AIC_c) relating the Euclidean distance between population niche centroids (DBC), for each species pair, to lake mean depth (MeanD), surface area (SA), Secchi depth, shoreline fractal ratio (FR), growing degree days (GDD), and latitude. K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights, Adj-R^2 = adjusted R^2.

Model Predictors and Coefficients	Rank	K	AICc	Δ_i	w_i	Adj R2
BURBOT - LAKE TROUT						
Intercept	2	1	56.37	0.00	0.19	0.00
Log(Lat)(-0.14)	3	2	57.51	1.14	0.11	0.01
Log(Secchi)(0.14)	3	3	57.53	1.16	0.11	0.01
Log(FR)(-0.11)	3	4	58.10	1.73	0.08	-0.01
Log(MeanD)(0.09)	3	5	58.34	1.98	0.07	-0.02
Log(GDD)(0.07)	3	6	58.62	2.26	0.06	-0.03
Log(SA)(-0.02)	3	7	58.89	2.52	0.05	-0.04
Log(Secchi)(0.16),Log(FR)(-0.14)	4	8	59.05	2.68	0.05	0.02
Log(Lat)(-0.15), Log(FR)(-0.11)	4	9	59.37	3.00	0.04	0.01
Log(Lat)(-0.11), Log(0.10)	4	10	59.65	3.28	0.04	0.00
Log(Lat)(-0.13), Log(0.07)	4	11	59.91	3.54	0.03	-0.01
Log(Secchi)(0.13), Log(MeanD)(0.06)	4	12	60.03	3.67	0.03	-0.02
Log(Secchi)(0.16), Log(SA)(-0.05)	4	13	60.12	3.75	0.03	-0.02
Log(Lat)(-0.16), Log(SA)(0.04)	4	14	60.19	3.83	0.03	-0.03
Log(FR)(-0.11), Log(GDD)(0.06)	4	15	60.65	4.28	0.02	-0.04
Log(FR)(-0.11), Log(SA)(-0.01)	4	16	60.86	4.49	0.02	-0.05
Log(MeanD)(0.11), Log(SA)(-0.05)	4	17	60.96	4.60	0.02	-0.05
Log(GDD)(0.07), Log(SA)(-0.02)	4	18	61.38	5.02	0.02	-0.07
BURBOT - NORTHERN PIKE						
Log(MeanD)(0.60)	3	1	83.11	0.00	0.34	0.23
Log(MeanD)(0.55), Log(Secchi)(0.21)	4	2	84.74	1.63	0.15	0.23
Log(MeanD)(0.61), Log(Lat)(0.08)	4	3	85.72	2.61	0.09	0.20
Log(Secchi)(0.41), Log(FR)(-0.05)	4	4	85.85	2.75	0.09	0.20
Log(MeanD)(0.60), Log(SA)(-0.02)	4	5	85.87	2.77	0.09	0.20
Log(FR)(-0.41), Log(GDD)(0.37)	4	6	86.64	3.53	0.06	0.18
Log(FR)(-0.44)	3	7	87.09	3.98	0.05	0.11
Log(GDD)(0.40)	3	8	87.93	4.82	0.03	0.08
Intercept	2	9	88.68	5.58	0.02	0.00
Log(Secchi)(0.33)	3	10	88.96	5.85	0.02	0.04
Log(FR)(-0.45), Log(SA)(0.18)	4	11	89.15	6.04	0.02	0.09
Log(FR)(-0.44), Log(-0.02)	4	12	89.86	6.75	0.01	0.07
Log(GDD)(0.41), Log(SA)(0.18)	4	13	90.01	6.90	0.01	0.07
Log(SA)(0.15)	3	14	90.77	7.66	0.01	-0.02

Model Predictors and Coefficients	Rank	K	AICc	Δ_i	w_i	Adj R2
Log(Lat)(0.00)	3	15	91.23	8.12	0.01	-0.04
Log(Secchi)(0.39), Log(Lat)(0.15)	4	16	91.34	8.23	0.01	0.02
Log(Secchi)(0.31), Log(SA)(0.08)	4	17	91.59	8.48	0.00	0.01
Log(SA)(0.18), Log(Lat)(-0.07)	4	18	93.46	10.35	0.00	-0.06
BURBOT - WALLEYE						
Log(GDD)(0.42), Log(FR)(-0.31)	4	1	36.62	0.00	0.56	0.61
Log(MeanD)(0.48), Log(SA)(-0.40)	4	2	37.55	0.92	0.36	0.59
Log(GDD)(0.43), Log(SA)(-0.24)	4	3	42.27	5.65	0.03	0.52
Log(Lat)(-0.37), Log(FR)(-0.35)	4	4	42.46	5.84	0.03	0.51
Log(MeanD)(0.33), Log(Lat)(-0.31)	4	5	44.72	8.10	0.01	0.47
Log(GDD)(0.44)	3	6	46.15	9.52	0.00	0.41
Log(FR)(-0.38), Log(Secchi)(0.25)	4	7	50.74	14.12	0.00	0.34
Log(FR)(-0.33), Log(SA)(-0.25)	4	8	50.82	14.20	0.00	0.34
Log(MeanD)(0.37)	3	9	51.63	15.00	0.00	0.27
Log(Lat)(-0.36)	3	10	52.44	15.82	0.00	0.25
Log(MeanD)(0.34), Log(Secchi)(0.12)	4	11	53.28	16.65	0.00	0.27
Log(FR)(-0.34)	3	12	53.34	16.72	0.00	0.23
Log(Lat)(-0.30), Log(SA)(-0.15)	4	13	53.52	16.89	0.00	0.27
Log(SA)(-0.32), Log(Secchi)(0.26)	4	14	54.59	17.96	0.00	0.24
Log(Lat)(-0.33), Log(Secchi)(0.07)	4	15	54.92	18.29	0.00	0.23
Log(SA)(-0.26)	3	16	56.87	20.25	0.00	0.12
Intercept	2	17	58.79	22.16	0.00	0.00
Log(Secchi)(0.19)	3	18	59.02	22.39	0.00	0.05
LAKE TROUT - NORTHERN PIKE						
Log(Lat)(0.17), Log(MeanD)(0.14)	4	1	32.38	0.00	0.21	0.17
Log(Lat)(0.15)	3	2	33.16	0.78	0.14	0.09
Intercept	2	3	34.15	1.77	0.09	0.00
Log(MeanD)(0.12)	3	4	34.52	2.14	0.07	0.04
Log(SA)(0.11)	3	5	34.73	2.35	0.07	0.03
Log(Lat)(0.18), Log(Secchi)(0.09)	4	6	34.73	2.35	0.07	0.09
Log(Lat)(0.15), Log(FR)(-0.08)	4	7	34.83	2.45	0.06	0.09
Log(Lat)(0.12), Log(SA)(0.07)	4	8	35.27	2.89	0.05	0.07
Log(FR)	3	9	35.62	3.25	0.04	0.00
Log(MeanD)(0.09), Log(SA)(0.09)	4	10	36.17	3.79	0.03	0.04
Log(SA)(0.12), Log(FR)(-0.09)	4	11	36.18	3.80	0.03	0.04
Log(GDD)(-0.05)	3	12	36.25	3.88	0.03	-0.02
Log(Secchi)(0.02)	3	13	36.63	4.26	0.03	-0.04
Log(SA)(0.11), Log(GDD)(-0.05)	4	14	37.14	4.76	0.02	0.01
Log(MeanD)(0.12), Log(Secchi)(-0.01)	4	15	37.28	4.91	0.02	0.00
Log(SA)(0.11), Log(Secchi)(-0.01)	4	16	37.50	5.12	0.02	-0.01

Model Predictors and Coefficients	Rank	K	AICc	Δ_i	w_i	Adj R2
Log(FR)(-0.09), Log(GDD)(-0.06)	4	17	37.82	5.45	0.01	-0.02
Log(FR)(-0.09), Log(Secchi)(0.03)	4	18	38.24	5.86	0.01	-0.04
LAKE TROUT - WALLEYE						
Log(FR)(-0.14), Log(Secchi)(0.13)	4	1	26.46	0.00	0.19	0.16
Log(FR)(-0.12)	3	2	27.59	1.13	0.11	0.07
Intercept	2	3	28.03	1.57	0.09	0.00
Log(Secchi)(0.11)	3	4	28.11	1.65	0.08	0.05
Log(MeanD)(0.11)	3	5	28.21	1.75	0.08	0.05
Log(MeanD)(0.14), Log(SA)(-0.11)	4	6	28.66	2.20	0.06	0.09
Log(Secchi)(0.13), Log(SA)(-0.10)	4	7	28.94	2.48	0.06	0.08
Log(Secchi)(0.09), Log(MeanD)(0.09)	4	8	29.28	2.82	0.05	0.07
Log(FR)(-0.12), Log(SA)(-0.06)	4	9	29.53	3.08	0.04	0.06
Log(FR)(-0.12), Log(Lat)(-0.06)	4	10	29.65	3.20	0.04	0.06
Log(SA)(-0.07)	3	11	29.67	3.21	0.04	-0.01
Log(Lat)(-0.05)	3	12	30.01	3.55	0.03	-0.02
Log(FR)(-0.12), Log(GDD)(0.04)	4	13	30.07	3.62	0.03	0.04
Log(GDD)(0.05)	3	14	30.16	3.70	0.03	-0.02
Log(MeanD)(0.10), Log(Lat)(-0.04)	4	15	30.66	4.20	0.02	0.02
Log(Secchi)(0.11), Log(Lat)(-0.01)	4	16	30.85	4.40	0.02	0.01
Log(SA)(-0.07), Log(GDD)(0.04)	4	17	32.08	5.63	0.01	-0.03
Log(SA)(-0.06), Log(Lat)(-0.03)	4	18	32.25	5.79	0.01	-0.04
NORTHERN PIKE - WALLEYE						
Log(Lat)(0.37), Log(Secchi)(0.26)	4	1	44.35	0.00	0.34	0.33
Log(Lat)(0.31), Log(MeanD)(0.23)	4	2	44.91	0.56	0.26	0.31
Log(SA)(0.21), Log(Lat)(0.20)	4	3	46.89	2.54	0.10	0.26
Log(SA)(0.28)	3	4	47.64	3.29	0.07	0.19
Log(Lat)(0.27)	3	5	48.00	3.65	0.05	0.18
Log(SA)(0.29), Log(FR)(-0.15)	4	6	48.05	3.71	0.05	0.23
Log(SA)(0.25), Log(MeanD)(0.12)	4	7	49.00	4.65	0.03	0.20
Log(Lat)(0.27), Log(FR)(-0.13)	4	8	49.10	4.75	0.03	0.20
Log(SA)(0.27), Log(Secchi)(0.06)	4	9	50.08	5.73	0.02	0.17
Log(SA)(0.28), Log(GDD)(0.00)	4	10	50.42	6.07	0.02	0.16
Log(MeanD)(0.19)	3	11	51.43	7.09	0.01	0.07
Intercept	2	12	51.91	7.56	0.01	0.00
Log(FR)(-0.14)	3	13	52.99	8.64	0.00	0.01
Log(Secchi)(0.12)	3	14	53.36	9.01	0.00	0.00
Log(MeanD)(0.18), Log(Secchi)(0.08)	4	15	53.69	9.34	0.00	0.05
Log(FR)(-0.16), Log(Secchi)(0.14)	4	16	54.12	9.78	0.00	0.03
Log(GDD)(-0.02)	3	17	54.43	10.08	0.00	-0.04
Log(FR)(-0.14)	4	18	55.70	11.35	0.00	-0.02

APPENDIX B:

SUPPLEMENTARY TABLES FOR CHAPTER 2

Table B1 Summary table of nine models ranked by second order Akaike Information Criterion (AIC_c) relating mean total mercury in a 500 g fish to Species (class variable), trophic position (lake-standardized residuals; $\delta^{15}N$), energy source (lake-standardized residuals; $\delta^{13}C$), and lifetime growth rate (lake-standardized residuals; LGR). Each model had a random effect term specified by Lake (random intercept), and all models, except the species fixed effects model, also included a random slope term representing species (random slope). K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights (%), R^2_{Marg} = marginal R^2 and R^2_{Cond} = conditional R^2. n = 13 lakes.

Fixed Effects and Standardized Coefficients	Rank	K	AICc	Δ_i	w_i	R^2_{Marg}	R^2_{Cond}
$\delta^{15}N$ (0.09)	1	5	-50.26	0.00	0.75	0.14	0.85
$\delta^{15}N$ (0.10), $\delta^{13}C$ (0.03)	2	7	-46.89	3.37	0.14	0.15	0.86
$\delta^{15}N$ (0.07), LGR (-0.02)	3	7	-46.12	4.15	0.09	0.15	0.85
$\delta^{15}N$ (0.08), $\delta^{13}C$ (0.03), LGR (-0.02)	4	9	-42.24	8.02	0.01	0.16	0.86
Species	5	6	-34.92	15.34	0.00	0.27	0.72
$\delta^{13}C$ (0.07), LGR (-0.09)	6	7	-27.14	23.13	0.00	0.13	0.73
LGR (-0.07)	7	5	-26.89	23.38	0.00	0.11	0.66
$\delta^{13}C$ (0.06)	8	5	-18.83	31.43	0.00	0.06	0.73
Intercept	9	3	-11.02	39.24	0.00	0.00	0.36

Table B2 Summary table of nine models ranked by second order Akaike Information Criterion (AIC_c) relating mean total mercury in a 1500 g fish to Species (class variable), trophic position (lake-standardized residuals; $\delta^{15}N$), energy source (lake-standardized residuals; $\delta^{13}C$), and lifetime growth rate (lake-standardized residuals; LGR). Each model had a random effect term specified by Lake (random intercept), and all models, except the species fixed effects model, also included a random slope term representing species (random slope). K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights (%), R^2_{Marg} = marginal R^2 and R^2_{Cond} = conditional R^2. n = 21 lakes.

Fixed Effects and Standardized Coefficients	Rank	K	AICc	Δ_i	w_i	R^2_{Marg}	R^2_{Cond}
Species	1	6	-11.97	0	0.35	0.19	0.61
$\delta^{15}N$ (-0.02), LGR (-0.8)	2	7	-11.55	0.41	0.29	0.06	0.66
$\delta^{15}N$ (0.03)	3	5	-10.50	1.47	0.17	0.02	0.64
$\delta^{13}C$ (0.03), LGR (-0.10)	4	7	-9.02	2.95	0.08	0.11	0.63
LGR (-0.07)	5	5	-8.09	3.87	0.05	0.07	0.64
$\delta^{15}N$ (-0.01), $\delta^{13}C$ (-0.03), LGR (-0.08)	6	9	-7.35	4.62	0.03	0.06	0.64
$\delta^{15}N$ (0.04), $\delta^{13}C$ (0.01)	7	7	-6.82	5.15	0.03	0.02	0.63
$\delta^{13}C$ (0.00)	8	5	3.50	15.47	0.00	0.00	0.54
Intercept	9	3	12.19	24.16	0.00	0.00	0.36

Table B3 Summary table of nine models ranked by second order Akaike Information Criterion (AICc) relating mean total mercury in a 1 kg fish to Species (class variable), trophic position (baseline adjusted; $\delta^{15}N_{adj}$), energy source (percent benthic carbon; PB), and lifetime growth rate (lake-standardized residuals; LGR). Each model had a random effect term specified by Lake (random intercept), and all models, except the species fixed effects model, also included a random slope term representing species (random slope). K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights (%), R^2_{Marg} = marginal R^2 and R^2_{Cond} = conditional R^2. n = 7 lakes.

Fixed Effects and Standardized Coefficients	Rank	K	AIC_c	Δ_i	w_i	R^2_{Marg}	R^2_{Cond}
LGR (-0.11)	1	5	-15.27	0.00	0.91	0.24	0.74
LGR (-0.12), $\delta^{15}N_{adj}$ (-0.01)	2	7	-8.83	6.44	0.04	0.25	0.75
LGR (-0.11), PB (0.01)	3	7	-8.42	6.85	0.03	0.25	0.73
$\delta^{15}N_{adj}$ (0.10)	4	5	-7.36	7.91	0.02	0.14	0.80
PB (-0.10)	5	5	-3.95	11.32	0.00	0.14	0.73
$\delta^{15}N_{adj}$ (0.07), PB (-0.06)	6	7	-2.49	12.78	0.00	0.18	0.84
Intercept	7	3	-0.76	14.51	0.00	0.00	0.47
$\delta^{15}N_{adj}$ (-0.01), PB (0.00), LGR (-0.11)	8	9	-0.44	14.83	0.00	0.24	0.76
Species	9	6	7.14	22.41	0.00	0.17	0.67

Table B4 Summary table of nine models ranked by second order Akaike Information Criterion (AIC_c) relating mean total mercury in a 1 kg fish to Species (class variable), trophic position (lake-standardized residuals; $\delta^{15}N$), energy source (lake-standardized residuals; $\delta^{13}C$), and lifetime growth rate (lake-standardized residuals; LGR). Each model had a random effect term specified by Lake (random intercept), and all models, except the species fixed effects model, also included a random slope term representing species (random slope). K = total number of parameters, Δ_i = Akaike differences, w_i = Akaike weights (%), R^2_{Marg} = marginal R^2 and R^2_{Cond} = conditional R^2. n = 7 lakes.

Fixed Effects and Standardized Coefficients	Rank	K	AICc	Δ_i	w_i	R^2_{Marg}	R^2_{Cond}
LGR (-0.11)	1	5	-15.27	0.00	0.63	0.24	0.74
$\delta^{15}N$ (0.11), $\delta^{13}C$ (-0.07)	2	7	-12.19	3.08	0.14	0.35	0.91
$\delta^{13}C$ (-0.04), LGR (-0.11)	3	7	-11.59	3.69	0.10	0.33	0.86
$\delta^{15}N$ (0.09)	4	5	-10.33	4.94	0.05	0.16	0.74
$\delta^{15}N$ (0.02), LGR (-0.09)	5	7	-8.96	6.31	0.03	0.23	0.78
$\delta^{13}C$ (-0.09)	6	5	-8.38	6.89	0.02	0.17	0.64
Species	7	6	-7.73	7.54	0.01	0.20	0.68
$\delta^{15}N$ (-0.05), $\delta^{13}C$ (0.07), LGR (-0.06)	8	9	-7.48	7.79	0.01	0.38	0.92
Intercept	9	3	-4.40	10.87	0.00	0.00	0.42